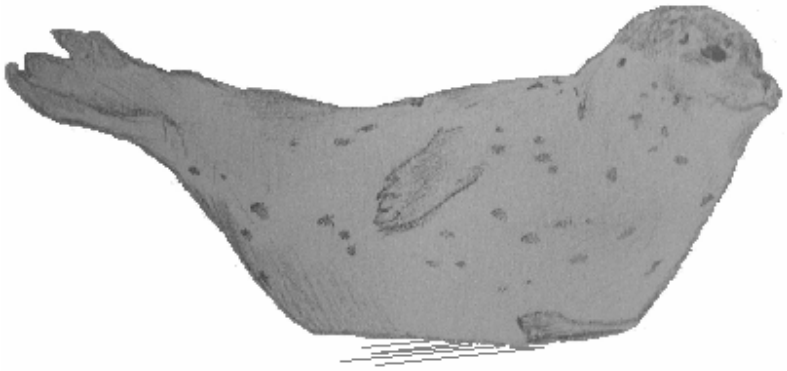
Population Dynamics of Harbour Seals, *Phoca vitulina* L.,

Master of Science Thesis 2007

Marijana Brkljacic



Forord

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ABSTRACT

In order to identify the dynamics regulating growth and viability in a harbour seal population, a combination of analytical and simulation methods is applied. Initially, an equilibrium population with stable age distribution was constructed by means of the age-specific parameters natural mortalities (m), sexual maturities (f) and fertility (b). To prevent indefinite population growth, density dependence was integrated by specifying a carrying capacity (K) of the habitat and alternative parameter values in accordance to changing population densities. A sensitivity analysis was then carried out; measuring which of the demographic parameters had the most profound effects on population growth. To assess this further, we evaluated whether the age structured model may be approximated by the simpler logistic model relying on a single parameter: the intrinsic growth rate. Finally, a more realistic harbour seal population was modelled, in which colonies of various sizes were given different demographic parameter values to mimic the typical source-sink dynamics often found in metapopulations. The effect of environmental stochasticity was explored by running a selection of computer simulations, incorporating random mortality- and emigration rates and catastrophic events.

The simulations indicated that population growth is most sensitive to changes in age at sexual maturity along with natural mortality of pups and in seals from two years of age and older. When comparing the growth models, it became clear that the simple logistic model may be used to describe a population subject to density dependent growth, such as a harbour seal population. However, both models had a severe constraint; the convergence to equilibrium (i.e. carrying capacity) was unrealistically slow. To avoid this, subsequent simulations assessing metapopulation dynamics were given a constant growth rate. The dynamics of the largest main colony (i.e. source) were independent of that of the remaining smaller satellite colonies, acting more or less as sinks. For these colonies, however, the opposite relationship could be observed. Given that the satellite colonies differed in size and inner recruitment, their dependence of dispersers from the main colony varied correspondingly. Random mortality had the greatest effect on the colonies with the fewest animals, displayed through erratic fluctuations and turnover

events (i.e. instability). The largest satellites maintained a relatively stable colony structure provided that the random mortality rates did not exceed the immigration recruitment from the source colony. During the rebuilding process following a catastrophic event, stochastic mortality effectively impeded population growth in all the satellite colonies. Overall, the simulations demonstrate how different aspects of population dynamics may control population growth and why small or fragmented populations are especially vulnerable to environmental stochasticity.

INTRODUCTION

Why do population numbers vary in time and space, and which mechanisms influence the observed pattern of population change? The study of population dynamics seek to explain these questions and it has a fundamental role within the ecology of species. Central aspects regarding population dynamics are thus related to growth and abundance (i.e. size). Population growth rates and population size are in turn the result of several intrinsic population characters, such as age specific fertility and mortality rates. No population, however, is an isolated entity unaffected by extrinsic factors; hence population dynamics should be viewed in close relationship with the ecosystem. The environment is rarely, if ever, stable, and populations will occasionally reflect their surroundings by showing changes in abundance and viability. Fluxes in food availability, infectious diseases and hunting may have significant impacts on population dynamics in pinniped populations. The unpredictable nature of the environment imposes perhaps the biggest threat towards populations of limited size and those suffering from fragmentation. For instance, harbour seals are occasionally found scattered in small groups separated by considerable distances from larger colonies, this being the case of those inhabiting the coast of Southern Norway. Such small colonies may run a risk of extinction due to stochastic events alone. By studying the factors that affect growth, stability and decline of populations and how these interact, one might be able to understand current and future status of harbour seal populations.

The main objective of the present study is to examine some of the vital processes governing the population dynamics of harbour seals. A primary goal is to obtain the significance of various intrinsic factors in relation to population growth. For instance, which demographic parameters may foster the highest population increase when assuming density dependence? Knowing that growth is considerably affected by a complex combination of age specific features, one might expect that such information is required when assessing population growth trends. However, age-specific data are not necessarily easily at hand, hence it is necessary to find an alternative approach that essentially describes the same growth behaviour as would an age specific approach. It is

also important to investigate the influence of external factors like environmental stochasticity, and how this may affect a harbour seal population subdivided into colonies of various sizes (i.e. metapopulation). Thus different aspects of size, migration, stability and persistence can be reviewed.

In an attempt to address these issues, a series of simulations was conducted and subsequently compared with actual pinniped populations. The main focus is attended to harbour seals inhabiting the Kattegat-Skagerrak area, and especially those found in Norwegian parts.

Global distribution

The harbour seal (*Phoca vitulina* L.), also known as the common seal, is a species belonging to the family "true" seals, Phocidae. Its distribution in the northern hemisphere, from the arctic to temperate regions, makes the harbour seal the most widespread of all pinnipeds (Thompson *et al.* 1997; Goodman 1998). Five subspecies are recognized to belong to this species, and the division between the various subspecies is made primarily on the basis of geographical distribution (King 1983). In the Northeast Atlantic, the harbour seals belong to the subspecies *Phoca vitulina vitulina*.

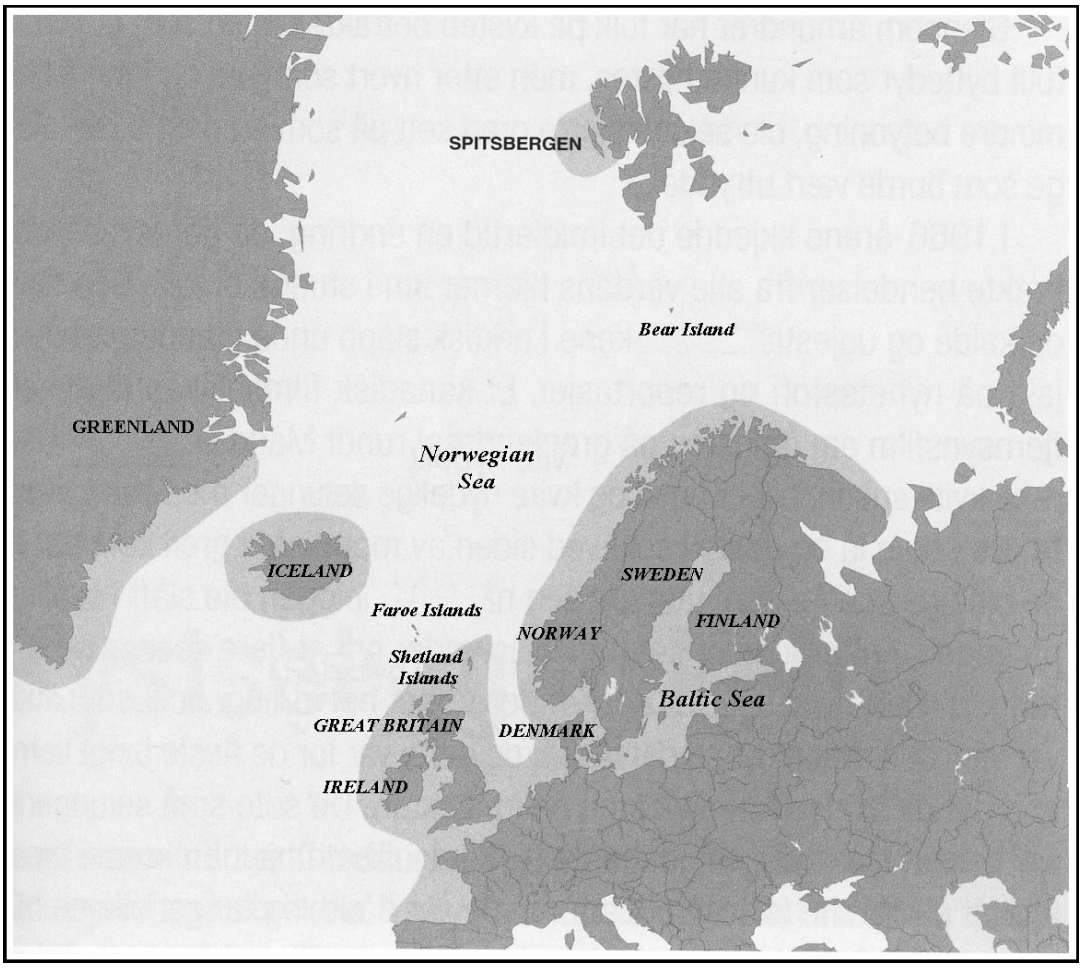

Figure 1. Distribution of harbour seals (*Phoca vitulina*) in the Eastern Atlantic (Henriksen & Røv 2004).

The distribution of *P. v. vitulina* (Figure 1) extends from the northernmost colony at Svalbard to Iceland, along the Norwegian coast and further into the Kattegat-Skagerrak, including the south-western Baltic Sea. Further they inhabit the Wadden Sea along the shores of Germany and The Netherlands, around the British Isles and southward to France (Härkönen and Heide-Jørgensen 1990; Henriksen and Røv 2004). Some animals may stray beyond the normal distribution, and occasionally seals have been observed as far south as Portugal (Bigg 1981). It is thought that approximately 50.000 seals inhabit the Eastern Atlantic (Dietz *et al.* 1989).

On the other side of the Atlantic, along the coast of Eastern North America, we find *P. v. concolor*. This subspecies occur from the Canadian sub-arctic and Greenland to northern Florida (Härkönen and Heide-Jørgensen 1990). A small population of the freshwater subspecies *P. v. mellonae* is present on the Ungava Peninsula (Canada). Its taxonomic status is somewhat unclear and is in some literature not regarded as a separate subspecies, but rather belonging to *P. v. concolor* (King 1983).

The last two subspecies are found in the Pacific, namely *P. v. richardsi* and *P. v. stejnegeri*. The former subspecies is also known as the Northeastern Pacific harbour seal, and it inhabits the North American coast from Alaska to Baja California (Härkönen and Heide-Jørgensen 1990). *P. v. stejnegeri*, on the other hand, lives in the Northwestern Pacific along the coasts from Kamchatka (Russia) down to the northern parts of Japan (Härkönen and Heide-Jørgensen 1990). There are no proper estimates of the present status of harbour seals worldwide, but according to Folkens and Reeves (2002), they number half a million or more throughout their range.

General life-history features and ecology

Distributed from the cold shores of the artic to temperate coasts, the harbour seal populates a wide variety of ecosystems and habitats. These habitats range from soft sediments of tidal mud and sandbanks, to rocky shores of coastal archipelagos and fjords. Not unexpectedly, the geographical distribution of harbours seals finds expression in not only appearance and physiology, but also in behaviour and hence life history.

The semi aquatic harbour seal is a relatively small phocid that, with its round head and short body, has an overall robust appearance (Bigg 1981). Colour and pattern of the pelage vary considerably between individual animals, and even between sexes. The ground colour ranges from white-grey or silver to dark brown and black, and is covered by small markings shaped like spots and rings with similar colour variability (Bigg 1981; Folkens and Reeves 2002). Unlike other species in the genus *Phoca*, harbour seal pups shed their embryonal white coat (lanugo) while still in their mother's womb (Bjørge 1993). They are thus born with a pelage that resemble that of the adults, making them prepared to swim shortly after birth (King 1983).

Even though the harbour seal tends to be solitary at sea, it is quite gregarious when hauled out. The number of animals on land varies considerably, and group sizes may in some protected estuaries count up to several thousand (e.g. in Alaska). Factors such as season, time of day, tidal cycles and weather conditions influence the number of harbour seals present on land (Thompson *et al.* 1989; Thompson and Miller 1990; Roen and Bjørge 1995). Nevertheless, the highest congregations are found to correlate with the reproductive cycle and moult (Härkönen 1987; Thompson *et al.* 1997).
A typical feature of harbour seals is that they utilize specific haul-out sites which they remain faithful to. This site fidelity, accompanied with the seals rather sedentary nature, pose specific requirements for the harbour seal habitat in terms of food availability and suitable haul-outs (Bjørge 1993). Although they are considered to be non-migratory with restricted movements only (Bigg 1981), young animals are known to disperse over longer distances (Wiig and Øien 1988; Thompson *et al.* 1994).

When it comes to body measures females are usually within 90 kg and 170 cm while males may exceed 180 cm and 100 kg (Henriksen 2000), although this may vary among the various subspecies. Despite these variations, harbour seals in the North Atlantic do not differ significantly from the other subspecies with respect to growth and reproduction (Härkönen and Heide-Jørgensen 1990). The body mass of adult seals fluctuates throughout the year, and weight loss is usually correlated with periods where a considerable amount of energy has to be allocated; during parturition, mating and moulting (Härkönen and Heide-Jørgensen 1990). When it comes to maximum longevity, it has been recorded to be 36 and 33 years for females and males, respectively (Härkönen and Heide-Jørgensen 1990).

Female harbour seals attain sexual maturity at 3-4 years of age, whereas males become mature at 4-6 years (Härkönen and Heide-Jørgensen 1990; Bjørge 1992). The age of sexual maturity is inevitably influenced by growth, and it appears that body size may be a better measurement for maturity than age (Sergeant 1978). Seasonal timing of the reproductive cycle differs between the different subspecies of which the mating season generally takes place from late spring through fall. In the Kattegat-Skagerrak region it occurs between July and August (Härkönen and Heide-Jørgensen 1990).

At the beginning of the breeding season females give birth to a single pup and most births take place in June and early July in the Northeast Atlantic (Bigg 1981; Thompson 1988; Härkönen and Heide-Jørgensen 1990). During lactation the mother and her pup build a close relationship, and the fact that harbour seal mothers tend to care for their offspring to a greater extent than other seals, undoubtedly increases their chance of survival (Henriksen and Røv 2004).

Mothers nurse their young in a period that lasts up to 3-5 weeks (Bjørge 1993) before being weaned and thus abandoned by their mother (Henriksen and Røv 2004). The pup gains just over half a kilo a day, and quickly doubles its initial birth weight of roughly 10 kg at the end of the lactation period (Henriksen and Røv 2004). Lactating females may have a weight loss up to 37% due to restricted foraging opportunities (Härkönen and

Heide-Jørgensen 1990), and to compensate for the great energy loss the mother starts to forage a few days after giving birth (Folkens and Reeves 2002). A study by Thompson *et al*. (1994) showed that pups born by small females have a lower rate of survival. This was probably due to the fact that the leaner females had to resume their feeding earlier in order to avoid starvation, as opposed to heavier females who could sustain suckling for a longer period of time.

Courtship and mating normally takes place in the water, and it is not unusual that the male is promiscuous, mating with several females during this period (Bigg 1981; Henriksen and Røv 2004). Males often vocalize and display to attract females' attention, but maybe just as important to intimidate rival males. Breeding is certainly a costly activity and the mating behaviour reduces the time spent foraging. Males may experience a weight loss close to 15% of their bodyweight due to the energy-expenditure affiliated with competition and copulation (Härkönen and Heide-Jørgensen 1990).

In the annual moult, occurring between spring and autumn, large aggregations of harbour seals can be seen basking in the sun. Moult typically takes place on specific haul-outs, and the peak moult in the Northeast Atlantic is between mid July and mid September, more or less at the same time as the mating (Bjørge 1993).

Feeding ecology

The harbour seal is a generalized predator. It is mainly piscivore, feeding on a wide variety of fish, but the diet may also include crustaceans and cephalopods, all depending on prey availability. Adult seals seem to prefer benthic and demersal fish species, such as codfish (Gadoids) and flatfishes (Pleuronectoids), but pelagic schooling fish may also be included in their diet (e.g. Clupeoids)(Härkönen 1987). Since the harbour seals are opportunistic predators, their diet often reflects both the seasonal availability and geographical distribution of prey species (Pierce *et al.* 1991; Olsen and Bjørge 1995; Tollit *et al.* 1997; Pierce and Santos 2003). It is believed that harbour seals consume 3-5 kg of fish on a daily basis when foraging actively (Ugland *et al.* 1984; Henriksen and Røv 2004). Feeding trips are usually in close vicinity to the haul-out, and studies of radio

tagged seals show that most activity is at a distance less than 50 km from the haul-out (Thompson and Miller 1990; Thompson *et al.* 1991).

General population dynamics and aspects regarding small populations

Different factors affecting size, distribution and viability are fundamental aspects regarding population dynamics. A population, in broad terms, is defined as a group of individuals of the same species occupying a defined area at the same time. However, drawing up the boundaries of an area is difficult, especially in the continuous marine habitat. Population ecologists often define a population by means of demography or genetics. From a demographic approach, a population may be characterized by population structure (i.e. age and gender) and dynamics (e.g. mortality and natality) relatively independent of other populations. Alternatively, differences in characteristics like allele-frequencies may be employed when distinguishing two groups as separate populations in terms of genetic features. On the other hand, movement and distribution of individuals is of considerable importance. The more limited the exchange between two groups, for example due to long distances, the more likely it is that they will represent separate populations.

At a basic level, the potential size of a given population is influenced by natality, mortality, emigration and immigration (Krebs 1994). These primary population parameters are essential in order to identify the cause of changes in abundance (e.g. population growth rate). Furthermore, population regulation, often in terms of density dependence, might influence demographic features. For example, high population densities may cause decreasing birth rates and/or increasing death rates as a result of food shortage or epidemic disease. Conversely, at low densities birth rates will be high and losses from disease and other causes will be low. In order to study population regulation it is important to know whether a population is subdivided or not. If this is proven to be the case, knowledge of how the patches are linked is needed (Kareiva 1990).

Metapopulation dynamics

Often a population will consist of several local populations, or so-called subpopulations. With regard to harbour seals, a subpopulation may be represented by a colony (usually a cluster of haul-out groups). To assess the dynamics of such spatially distributed populations, the concept of metapopulations has been developed (Levins 1969). Metapopulation ecology deals with migration and how it affects local dynamics, population extinction and the establishment of new local populations (Hanski 1999). The general idea behind this concept is that a population has a patchy distribution creating a collection of small groups within patches (i.e. subpopulations). Such groups, though separated, will usually have enough exchange to ensure that genetic differentiation among patches is avoided, but at the same time limited enough to allow each patch to be relatively independent demographically (Hunter 2002). If, however, the patches are well interconnected through extensive immigration and emigration, it should be regarded as a single large population rather than a metapopulation. On the other extreme, little or no exchange between patches will indicate distinct populations.

Within metapopulation dynamics, dispersal or migration is considered to be crucial, encompassing the concept of source and sink metapopulations. Some subpopulations are called sources, with a net dispersal of emigrants, while other subpopulations are sinks, which cannot maintain themselves without the immigration from other subpopulations. The two types of metapopulations thus represent two different kinds of processes, which are extinction and colonization. Sometimes sources and sinks are referred to as core and satellite subpopulations. Core subpopulations are likely to be large and self-supporting, which make them persistent for relatively long periods of time, while satellites are likely to be small and net sinks. In practice it is difficult to distinguish sinks from sources, not only because of difficulties related to the monitoring of movements between subpopulations, but also because environmental changes may swap their roles.

Another term regarding metapopulation dynamics is the turnover theory presented by Hanski and Simberloff (1997). Turnover refers to the events that make subpopulations to sometimes appear (e.g. colonization) and disappear (e.g. local extinction). Small-scale

extinction and colonization events will often balance one another, but when the rate of extinction exceeds the rate of colonization, the outcome may be critical.

Problems related to small or fragmented populations

The large populations and wide geographic distribution of harbour seals make the risk of extinction improbable; however, small and local populations are vulnerable. The smaller the population, the bigger the probability of extinction becomes due to chance. Nevertheless, random events do not discriminate between sex and reproductive status of individuals. Thus, the stochastic processes affecting population abundances are more significant in populations with limited size. Examples of depleted pinniped populations are the highly fragmented and endangered Mediterranean monk seal (*Monachus monachus*) (Reijnders *et al.* 1988; Durant and Harwood 1992) and the isolated Saimaa ringed seals (*Pusa hispida saimensis*) (Jarvinen and Varvio 1986).

Mark Shaffer (1981) classified four interacting processes that could lead to extinction of a population: Demographic, environmental and genetic stochasticity, and catastrophes. Demographic stochasticity refers to the consequences resulting from random variation in reproductive success and survival in individuals. In order to predict the outcome of demographic dynamics, estimates of demographic parameters such as size, sex and age structure within the population together with death and birth rates are employed. Environmental stochasticity, referring to fluctuations in environmental conditions, may also influence these demographic parameters. A related topic, often included in environmental stochasticity, is the sudden catastrophic events, such as epidemics or oil spills, which may wipe out large portions of a population.

Another concern about diminishing populations is the loss of genetic diversity, which is believed to have a negative impact on individual fitness. Random variation in a gene frequencies within a population (i.e. genetic stochasticity), may be caused by factors such as genetic drift, bottlenecks and inbreeding. Lack of genetic diversity may cause a number of harmful effects by limiting reproduction and the ability to adapt to changing

conditions. However, genetic depletion is beyond the objectives and scope of this thesis and will therefore not be further considered.

BACKGROUND MATERIAL AND METHODS

Study area

The Skagerrak and Kattegat connects with the North Sea in the west and the Baltic Sea in the east, and it runs between Norway, Denmark and Sweden. Often the Skagerrak is included in the North Sea, while the Kattegat is included in the Baltic (Svansson 1975).

Being a transitional zone, the hydrographical conditions in the Kattegat-Skagerrak are highly influenced by both the Baltic and the North Sea. Large amounts of the saline water of Atlantic origin entering the North Sea, passes through Skagerrak, where it mixes with the brackish water from the Baltic and Kattegat. From the shallow, exposed and sandy beaches of Denmark to the deep, rocky basin of the Norwegian Trench, the Kattegat and Skagerrak contains a variety of habitats. It is a highly productive area where the benthic and pelagic communities are coupled in the shallow parts of the sea. As a result a high biodiversity is supported, including all the harbour seal colonies that are found scattered along its coastlines (Figure 2).

Two extreme types of environments are found in the Kattegat-Skagerrak area. Skagerrak, with a mean depth of 200 m (max 725 m)(Hedstrøm 1994), predominantly features a rocky-shore habitat. Here harbour seals haul out on rocks and skerries often sheltered from the open ocean by the nearly continuous archipelago running along the coast. In Kattegat, on the other hand, the mean depth is about 23 m (max 130 m) (Hedstrøm 1994) where seals inhabit sandy shores and mudflats often surrounded by the shallow soft sea bottoms. Unlike most other harbour seal habitats, the Kattegat-Skagerrak area has a more or less negligible tidal activity (Härkönen 1987) making haul-out sites readily accessible at any time.

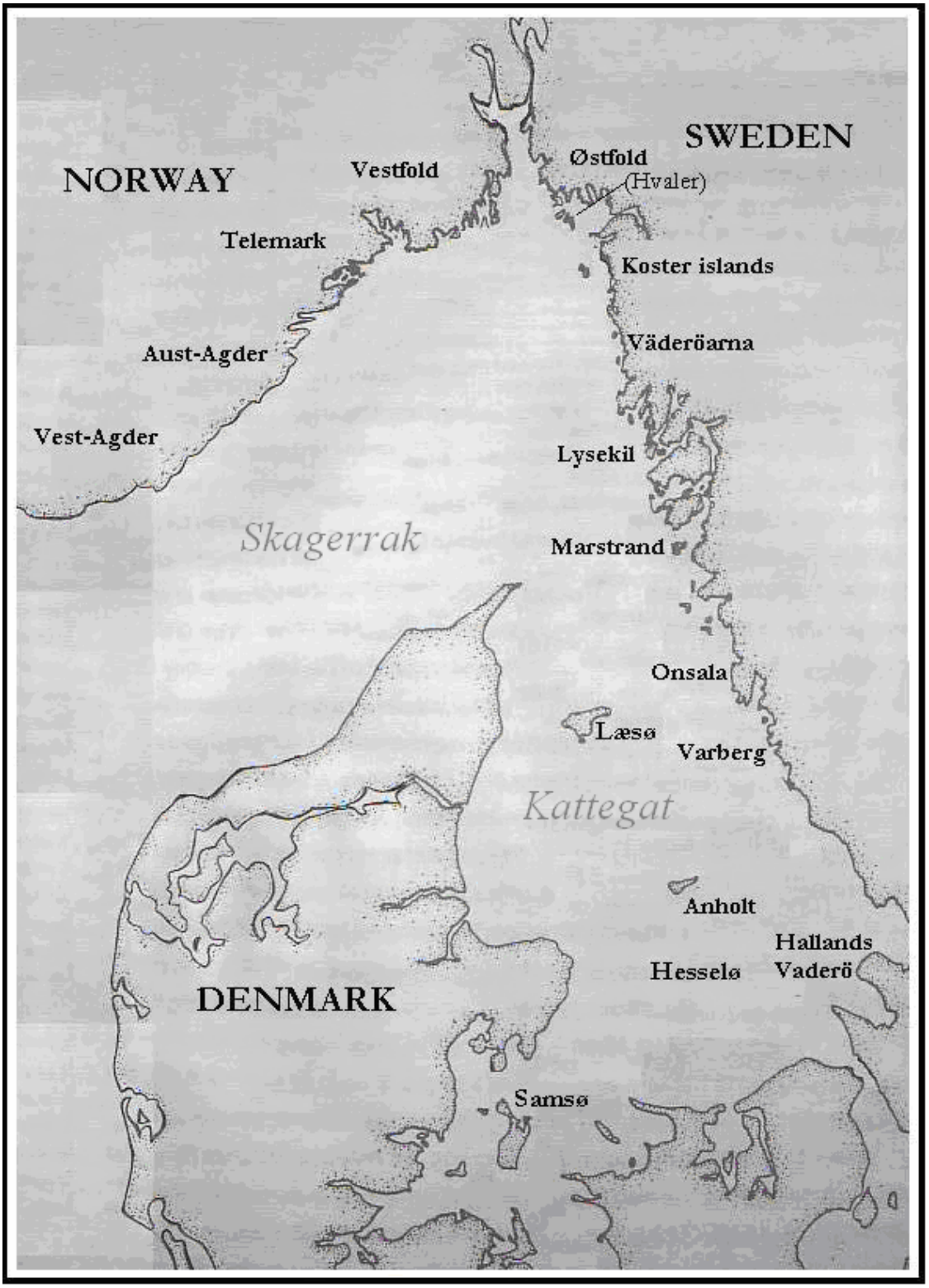

Figure 2. Harbour seal localities in the Kattegat-Skagerrak.

Collection of abundance data

The data on harbour seal abundances along the coasts of Skagerrak and Kattegat were obtained from counts carried out in the summer of 2006. Numbers were supplied by the Institute of Marine Research in Norway, the Swedish Museum of Natural History and the National Environmental Research Institute in Denmark. All surveys were conducted during the moulting season in late August, when the number of hauled-out harbour seals is shown to be at its peak (Heide-Jørgensen and Härkönen 1988). A summary of the counting surveys conducted in 2006 is listed in Table 1.

Skagerrak

In Norway the Skagerrak coast stretches from Vest-Agder County in the west to Østfold County in the east. The registrations of harbour seals at the Norwegian coast, with the exception of the Hvaler archipelago in Østfold, were carried out by boat. A thorough description of the counting methods employed is given in the annual report published by the Institute of Marine Research (Havforskningsinstituttet 2007).

The Swedish parts of Skagerrak include the country's northwest coast in the province of Böhuslen. Unlike the Norwegian surveys, data on seal abundances in Swedish Skagerrak were obtained by means of aerial surveys conducted during three days in August. For detailed description of the counting practice used, see Heide-Jørgensen and Härkönen (1988) and Härkönen *et al.* (2002).

Kattegat

The Kattegat runs between the south-western parts of Sweden and Denmark's east coast. Due to marked migrations and reciprocal exchange of animals between colonies, the seals populating Kattegat is considered to be a joint population of the two countries (Heide-Jørgensen and Dietz 1982). Counting surveys in this region are cooperatively carried out by the two neighbouring countries. The procedures employed are thus similar as those in Swedish Skagerrak. Description of the different haul-out sites in Kattegat are given in Heide-Jørgensen (1988).

All in all, a total of 8949 harbour seals were observed in Skagerrak and Kattegat during the summer moult in 2006. However, estimates of seal abundances made on the basis of actual counts represent only a minimum estimate. Studies conducted in Skagerrak by Härkönen *et al.* (1999) showed that seals counted during surveys represent roughly 56% of the true population size. If this is applied to the 2006 counts it gives a total population of about 16000 harbour seals in the Kattegat- Skagerrak area (Table 1).

Table 1. Occurrence of Harbour seals in the Kattegat-Skagerrak area according to surveys carried out in August 2006. "Number of harbour seals" represent actual counts of hauled out seals during the summer moult, while "Population Estimate" refers to the estimated population size when employing the assumed 56% haul-out fraction in accordance to Härkönen *et al.* (1999).

Region	Haul-out Area	Number of Harbour Seals	Population Estimate
Norwegian Skagerrak	**1.** Vest-Agder	0	
	2. Aust-Agder	10	
	3. Telemark	45	
	4. Vestfold	7	
	5. Buskerud/Oslo & Akershus*	–	
	6. Østfold (Hvaler)	266	
Swedish Skagerrak	**7.** Koster	995	
	8. Väderöarna	701	
	9. Lysekil	794	
	10. Marstrand	373	
Skagerrak		***3191***	***5698***
Swedish Kattegat	**11.** Onsala	1671	
	12. Vargberg	591	
	13. Hallans Väderö	652	
Danish Kattegat	**14.** Anholt	542	
	15. Hesselø	1052	
	16. Læsø	691	
	17. Samsø	559	
Kattegat		***5758***	***10282***
Total Kattegat-Skagerrak		**8949**	**15980**

***** No counting conducted; the occurrence of seals in this area is limited by some occasional animals at wintertime (Ugland et al. 1984).

Treatment of data

In order to identify the dynamics that might control a small or fragmented harbour seal population, an array of models were tested on various hypothetical colonies. The values of the parameters in the following population model and the alternative population growth rates are taken from various investigations of the population biology of the harbour seal (Bigg 1969; Heide-Jørgensen and Härkönen 1988; Allen *et al.* 1989; Markussen *et al.* 1989; Härkönen and Heide-Jørgensen 1990; Reijnders *et al.* 1997; van Haaften 1982; Härkönen 1987).

An obvious parameter of interest when studying changes in a population is the population's growth rate. In this study the growth rate was considered by using two different models, namely the *age structure model* and the alternative *logistic model*.

The age structured model

To assess the demographic features influencing population growth, and to which extent, we used an age structure model on a hypothetical harbour seal population. This model enabled us to model the effects of various age-specific factors on population size.

Calculating the stable age distribution

In order to construct an age structured model including density dependence, we initially want to obtain parameter values that induce population equilibrium (i.e. a stable age distribution). The age-specific parameters considered are natural mortality m, maturity rate f and fertility b.

Harbour seals have an average life expectancy of about 25 years. Accordingly, the model is set to contain 25 age classes: $i = 0, 1, 2, 3\ldots., 25$. When n_i is the numbers of individuals in age class i, then the total population size may be set as: $n = n_1 + \ldots + n_{25}$.

In seals, natural mortality is considerably higher for the youngest age groups compared to the older ones. The following mortality rates may therefore be reasonable to apply:

$m_0 = 0.35$, $m_1 = 0.5*m_0 = 0.175$ and $m_i = 0.12$ for all other age classes. Thus, the survival rate for pups younger than one year (m_0) is calculated to be $1 - m_0 = 1 - 0.35 = 0.65$, meaning that 65% of the pups will survive the first year, 82.5% will similarly survive their second year (i.e. between the ages of 1 and 2), while the subsequent age classes have a survival of 88%.

Like mortality, age at sexual maturity will differ between different age groups. In harbour seals age at sexual maturity is between 4 and 8 years. Hence the maturity rate is set to zero for the age groups 1-3, i.e. $f_1 = f_2 = f_3 = 0$. The fraction of mature seals, however, will have an increasing maturity from 10% in 4 year-olds up to 100% in 8 year-olds.
The maturity rate can be set as follows: $f_4 = 0.10$, $f_5 = 0.30$, $f_6 = 0.70$, $f_7 = 0.90$, $f_8 = 1$.
After the age of 8 all individuals are sexually mature, i.e. $f_i = 1$ for $i = 9, 10, 11, \ldots, 25$.
For the sake of simplicity, the age of maturation is equivalent to the age of first reproduction/parturition.

The final parameter to be considered is the fertility rate b, which represents the fraction of sexually mature individuals that participate in mating. Since the above parameter values are already given, the fertility rate has to be calculated in order to achieve population equilibrium. For doing so, essentially two requirements have to be met:

[1] The number of individuals in each age class should reflect the mortality rates, i.e. $n_{i+1} = (1 - m_i)*n_i$

[2] The pup production must reflect both the maturity rates as well as the fertility. In other terms, the number of pups produced by the i^{th} age class when the sex ratio is 1:1 (i.e. half of the individuals are females) may be set as:
$P_i = 0.5*b*f_i*n_i$

At equilibrium the number of pups, $P_4 + P_5 + \ldots + P_{25}$, produced by the age structure n_0, $n_1, n_2, \ldots, n_{25}$ must be equal to n_0, giving the following equation:

$$P_4 + P_5 + \ldots + P_{25} = n_0$$

By applying the formulas [1] and [2] in Excel, we find the fertility to be; $b = 0.80050836$ in the population at equilibrium state. Because the numbers of individuals in the various age classes occur linearly in the given equations, the pup production may be arbitrarily set to $n_0 = 1000$. The stable age structure, given in table 2, is obtained by combining the specified parameter values and the chosen pup production.

Table 2. A stable age distribution in a hypothetical harbour seal population at equilibrium. The following parameters have been used:
Natural mortality: $m_0 = 0.35$, $m_1 = 0.175$, and $m_i = 0.12$ for $i = 2, \ldots, 25$. Maturity rates: $f_1 = f_2 = f_3 = 0$, $f_4 = 0.10$, $f_5 = 0.30$, $f_6 = 0.70$, $f_7 = 0.90$, and $f_i = 1$ for $i = 8, \ldots, 25$. Fertility: $b = 0.80050836$. The number of pups, i.e. size of the 0-group, is arbitrarily set to 1000

Age	No. of individuals
0	1000
1	650
2	536
3	472
4	415
5	365
6	322
7	283
8	249
9	219
10	193
11	170
12	149
13	131
14	116
15	102
16	90
17	79
18	69
19	61
20	54
21	47
22	42
23	37
24	32
25	28
Total	**5911**

Incorporating density dependent parameters

Populations do not grow indefinitely seeing that many important processes are density dependent. When a population increases, it eventually reaches a limit imposed by inadequate resources and other environmental conditions. An undisturbed population may ultimately stabilize around a long term equilibrium, called the carrying capacity. The carrying capacity, K, is thus the maximum number of individuals that the environment can support.

Populations will normally fluctuate around the carrying capacity in response to changes in their environment. Due to the density dependent factors, populations may suffer from decreased birth rates and an increased risk of mortality. For instance, if food becomes less abundant or an epidemic breaks out, the population will decline. When circumstances return to normal, the population will rebuild towards its long term carrying capacity.

To incorporate density dependence in the age structured model, parameter values of natural mortality, sexual maturity and fertility are adjusted to simulate different population densities. In order to specify these dynamics, two relationships have to be considered:

(I) The extreme value of the parameter at a specified low level of population size relative to the carrying capacity.

(II) The value of the parameter as a function of population size relative to the carrying capacity at densities higher than specified above in (I).

Let us for instance consider the natural mortality of pups. When population sizes are low, one can easily imagine that the pups' survival will increase (e.g. more access to resources). Natural mortality, which was previously set to $m_0 = 0.35$, may then drop to some lower value, possibly as low as $m_0^* = 0.20$. At densities lower than 10% of the carrying capacity, we assume that the minimum value of mortality (i.e. $m_0 = 0.20$) is attained. Conversely, at densities 10% higher than the carrying capacity (termed D_{crit}) the equilibrium value of $m_0 = 0.35$ is attained. In other words, at densities lower than 10% of the carrying capacity 80% of the pups survive when compared with only 65% at the critical density, D_{crit}. The natural mortality of pups may be approximated by a linear increment (i.e. increase) from the extreme low value $m_0^* = 0.20$ to the equilibrium value $m_0 = 0.35$. The relationship between the density dependent parameter and the carrying capacity (described above) is: $n_{crit} = D_{crit} * K = 0.10 * K$

A similar procedure may be applied to the last two parameters: maturity and fertility. As opposed to natural mortality, these parameters will have a higher value at lower densities. Therefore the maximal values for maturity f_i^* ($i = 1, 2, \ldots, 25$) and fertility b^* must be specified, and a linear relationship between these extreme values and the equilibrium values may be assumed for higher densities. The dynamical properties of the age structured model are at this specified by the critical density and the extreme values of the natural mortalities, sexual maturities and fertility rates.

Sensitivity analysis of the parameters

In order to assess how changes in demographic parameters may influence the status of our population, a sensitivity analysis was carried out. This analysis enables the evaluation of how changes in for example survival or fecundities affect population growth when all other elements are kept constant. For example, are there any specific demographic parameters that have greater effect on population growth than others?

In this simulation series we began examining the effect of changes in age-specific factors on population growth rate by altering only a single parameter. Since the other parameters are kept constant (i. e. density independent) the influence of the examined parameter on the population growth can be revealed. The arbitrary value K = 1000 is chosen to represent the carrying capacity, while the critical density is set to be 10% of the carrying capacity (i.e. $D_{crit} = 0.10$). All simulations started out with an initial population size of 20 individuals projected 100 years ahead, incorporating various alternative extreme values of the parameters. The same simulations were repeated with each having a parameter showing alternative density dependence. Simulations with the following values were carried out:

1. Natural mortality of pups ($m_0^* = 0.30$, 0.25, 0.20 and 0.15)
2. Natural mortality of 1 year old seals ($m_1^* = 0.15$ and 0.125)
3. Natural mortality of seals 2 years of age and older ($m_i^* = 0.11$, 0.10 and 0.09)
4. Sexual maturity drops from the equilibrium value of six years to the alternative ages of five years ($f_4^* = 0.40$, $f_5^* = 0.70$, $f_6^* = 0.90$, $f_7^* = 1$) and four years ($f_4^* = f_5^* = f_6^* = f_7^* = 1$)
5. Fertility ($b^* = 0.85$, 0.90 and 0.95)

Approximations by the logistic growth model

Density dependent population growth is commonly represented by the logistic equation

[3] $N_{t+1} = N_t*[1 + r*(1 + N_t/K)]$,

where N_t is the population size at time t, K is the carrying capacity and r is the maximal population growth rate (i.e. intrinsic growth rate). While the age structured model has 25 age classes and 18 population parameters (i.e. density dependence in natural mortalities, sexual maturities and fertility rates), the logistic model simply considers all individuals as belonging to a single group. The logistic growth model has therefore only *one* parameter, which is the intrinsic growth rate. One may thus expect that the more sophisticated age structured model will exhibit a more complex behaviour than its simple logistic counterpart. In order to test this prediction, we compared the two alternative growth models by running a variety of simulations under different density dependent regimes.

All simulations were initiated with 20 individuals like before; only this time they were projected 200 years. The critical density and carrying capacity were once more set to $D_{crit} = 0.10$ and $K = 1000$ respectively, and the same parameter values for the equilibrium population were used. Various alternatives for the maximum change in the population parameters were examined as follows.

The first comparison between the two models was thought to simulate a slow growth rate. Here the logistic model was set to have an intrinsic growth rate of 4.2% ($r = 0.042$). In the aged structured model the density dependence in the natural mortalities are set to $m_0^* = 0.30$, $m_1^* = 0.15$, $m^* = 0.11$. Further, the sexual maturity was set to drop from 6 years at equilibrium ($f_4 = 0.10$, $f_5 = 0.30$, $f_6 = 0.70$, $f_7 = 0.90$, $f_8 = 1.00$) to 5 years at 10% of the carrying capacity ($f_4^* = 0.40$, $f_5^* = 0.70$, $f_6^* = 0.90$, $f_7^* = 1.00$, $f_8^* = 1.00$). Finally, the fertility rate was set to increase from $b = 0.80$ to $b^* = 0.85$.

In the second simulation the growth rate was set to show an intermediate growth. Now the intrinsic growth rate was amplified to 6.7% ($r = 0.067$). When it comes to the age

structured model the density dependent mortality rates were kept the same as in the previous simulation (see above). Sexual maturity, on the other hand, was reduced from 6 years at equilibrium ($f_4 = 0.10$, $f_5 = 0.30$, $f_6 = 0.70$, $f_7 = 0.90$, $f_8 = 1.00$) to 4 years at the critical density, i.e., 10% of the carrying capacity, ($f_4^* = f_5^* = f_6^* = f_7^* = f_8^* = 1.00$). When it comes to the fertility rate, it was increased from $b = 0.80$ to $b^* = 0.90$.

In the third and final comparison between the two density dependent growth models, the simulation was set to have a fast growth rate. This time the intrinsic growth rate was 10.5% (r = 0.105). The age structured model was further altered where natural mortalities were reduced to $m_0^* = 0.20$, $m_1^* = 0.125$, $m^* = 0.10$. Values of sexual maturity were the same as in the second simulation, while the fertility rate was slightly increased from $b = 0.80$ to $b^* = 0.95$.

Simulations assessing dynamics and viability in a harbour seal metapopulation

Although the demographic parameters described above had a significant role in shaping population growth, they do not fully explain the dynamics which are seen in natural populations. Two important elements which until now have not been considered in our models are dispersal and stochastic events. The main aim was to find out how the exchange of animals and sudden stochastic events (e.g. epidemics or oil spills) may influence the dynamics of a harbour seal metapopulation.

In the outer Oslo fjord there is one relatively large harbour seal colony residing at the Hvaler archipelago, while there are several smaller colonies scattered along the coast of Southern Norway (Table 1). On the basis of these fragmented colonies in the Norwegian Skagerrak, a hypothetical population model was created having the following features:

Population sizes: There are a total of 10 colonies in our model population. One colony, called the main or core colony, was constituted of 400 harbour seals. Further one colony had 50 individuals while two colonies had 25. The remaining six colonies were given a population size of 10 individuals each. The number of individuals was thought to represent the carrying capacity of a given colony, and this upper level was never

exceeded. The figures given above resemble those from earlier assessments conducted by Øynes in the 1960's (Øynes 1966), however, the size of the main colony is more in accordance with the present state.

Growth rates: Since we were primarily interested in studying the population fluctuations near a stable state or in the rebuilding process after a large impact, we applied a constant growth rate. Near the long term equilibrium level the main colony is given an annual growth of 2%, while the colonies with 25 or more seals are given a corresponding growth of 1%. Conversely, the smallest colonies with only 10 individuals are meant to behave stochastically and are therefore assigned a growth rate of zero. Under undisturbed conditions all animals above the carrying capacity were removed.

Mortality rates: A stochastic mortality rate was applied in all colonies except the main one. The parameter was termed random death, *RD*, and specifies the number of seals that are removed each year. In our simulation series we examined three alternative death rates; RD = 5, 8 and 12. Let us illustrate with an example. If random death is set to 5 (i.e., RD = 5) then 5 seals will be removed by randomly selecting between the nine colonies (recall that the main colony has no death rates). The colonies were selected with replacement meaning that any colony may lose all from none up to five seals in this stochastic death process.

Emigration rates: In order to replace the losses brought about by the random death rates, it is essential that the main colony recruits the other colonies. Therefore an emigration rate parameter, *ER,* was incorporated into the model, which represents the fraction of seals that each year leaves the main colony. Emigration rate was set to 0.02 (ER = 0.02) which means that the main colony annually loses 2% of its population through emigration to the other colonies. Thus, with an initial population size of 400 individuals, altogether 8 seals will disperse (400*0.02 = 8). The dispersal was conducted by eight colonies being selected at random, including replacement, and given a single seal.

Catastrophic event: A catastrophic event, such as an epidemic or an oil spill, may be modelled by specifying the colony sizes after the perturbation. In our simulation the main colony was set to be reduced from 400 individuals to 100 after a catastrophe, while the rest of the colonies were eradicated. This means that the main colony is the only one that remains and that nearly 80% of the initial population, as a whole is being wiped out.
It is important to consider the rate at which the population is restored to its original level. During the rebuilding process the intrinsic growth rate of the main colony was set to 5% while the number of emigrants continued to be 2% of the existing colony size as it grew. We studied the rebuilding process under three alternative values of random death:
RD = 0, 3 and 8.

With the parameters given above an infinite number of simulations could be carried out. However, our main aim was to catch the principles that lie beneath the dynamics of harbour seal populations being dispersed in colonies of various sizes. In order to do so, we primarily had to consider two circumstances that seem to govern the dynamics.

Initially we have the relationship between the growth rate and emigration rate of the main colony. Near the carrying capacity, it is reasonable to assume that these values are about equal. As a result we let ER = growth rate = 0.02 near equilibrium. After a heavy perturbation, the density dependent factors are likely to increase the growth rate. Under these circumstances we assumed a 5% growth rate in the rebuilding process.

Subsequently, since the main colony stands for the recruitment, the crucial factors will be the number of random deaths (RD) and the number of emigrants (ER) that the smaller colonies receive. We therefore chose to study the alternative random death values 0, 3, 5, 8 and 12. A value above 8 may be regarded as to simulate the negative effects resulting from a long term environmental change.

RESULTS

Sensitivity analysis of the parameters

1. Natural mortality of pups, m_0

A higher fraction of pups surviving their first year seems to have a profound effect on the growth of the population model. With the initial mortality rate among pups set to m_o = 0.35 at equilibrium, a reduction to the alternative density dependent values (i.e., m_o*= 0.30, 0.25, 0.20 and 0.15) resulted in an obvious increase in population size (Figure 3). For example, a maximum drop from 35% to 30% in the given parameter resulted in that the initial population size of 20 seals will only double within 50 years. However, if the pup mortality is further reduced to 20%, a near doubling will occur within 25 years, and by the time of 50 years become 3.5 times as large (Table 3).

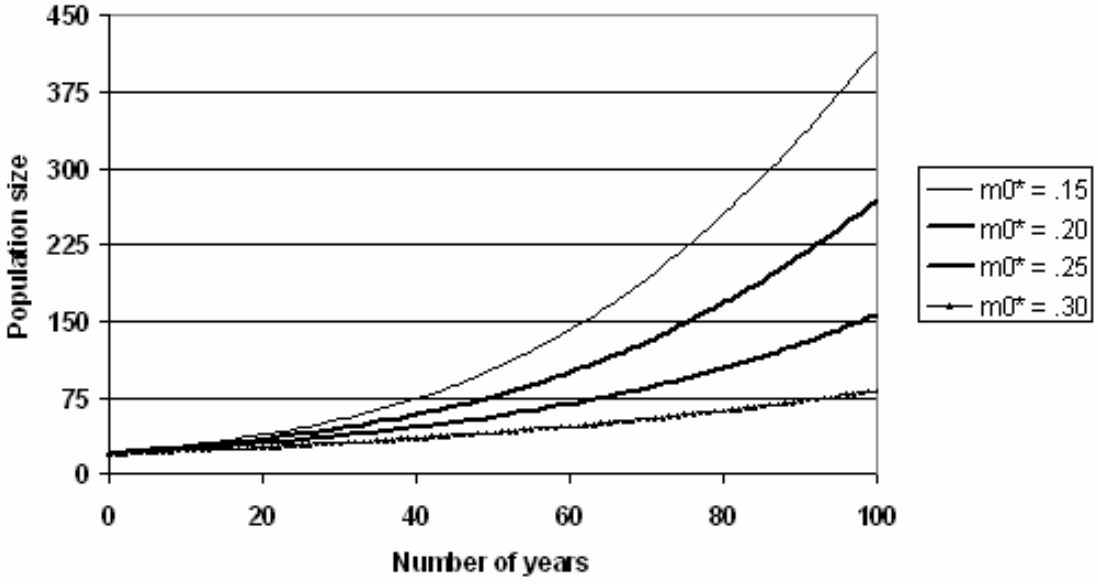

Figure 3. Effects on population growth when using the four alternative density dependent mortality rates of pups: m_0* = 0.30, 0.25, 0.20 and 0.15.

2. Natural mortality of 1 year old seals, m_1

Natural mortality among one year old seals has relatively minor effects on population size in our model. The initial population shows a rather slow growth in the course of 100 years (Figure 4) with the applied alternative mortality rates (i.e., $m_1^* = 0.15$ and $m_1^* = 0.125$). By comparison, density dependence in mortality in the second year has a much less effect on the population growth than variability in pup mortality (Table 3).

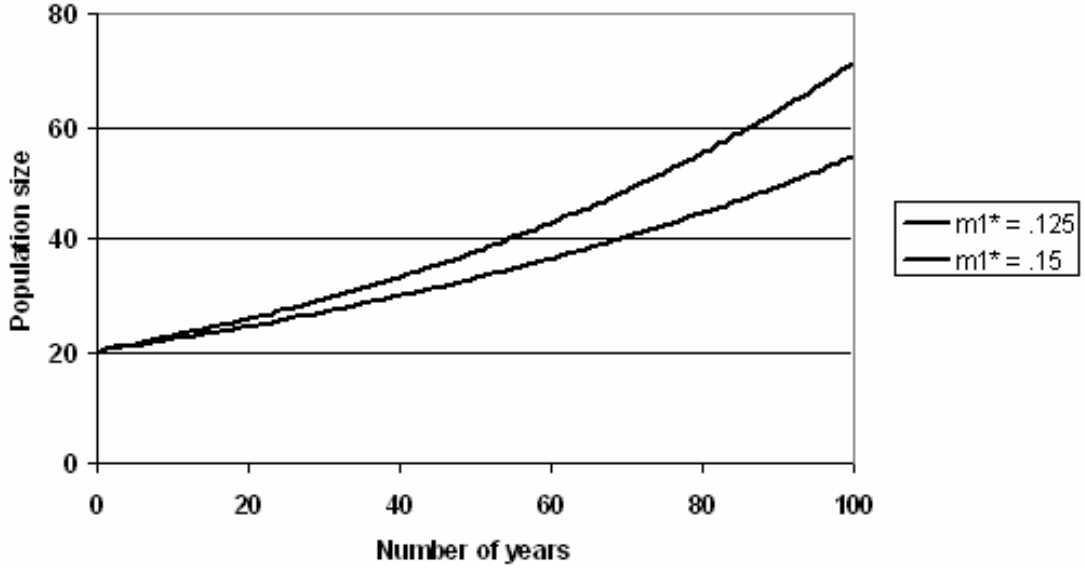

Figure 4. Effects on population growth when using the two alternative density dependent mortality rates of one year old seals: $m_1^* = 0.15$ and 0.125

3. Natural mortality of seals 2 years of age and older, *m*

Not surprisingly, a reduction in the natural mortality of seals from two years of age and older, which comprise about 70% of the total population (Table 2), may have a large impact on the growth of our hypothetical population. Again starting off with an original size of 20 individuals, the three population trajectories for the alternative mortality rates (i. e., $m^* = 0.11$, 0.10 and 0.09) demonstrate a clear increase throughout the years (Figure 5). Even a relatively small alteration from the equilibrium value of $m = 0.12$ (i.e. 12% mortality) to $m^* = 0.10$ will give a population almost twice the size within 25 years, and a further enlargement of 3.5 times within 50 years (Table 3).

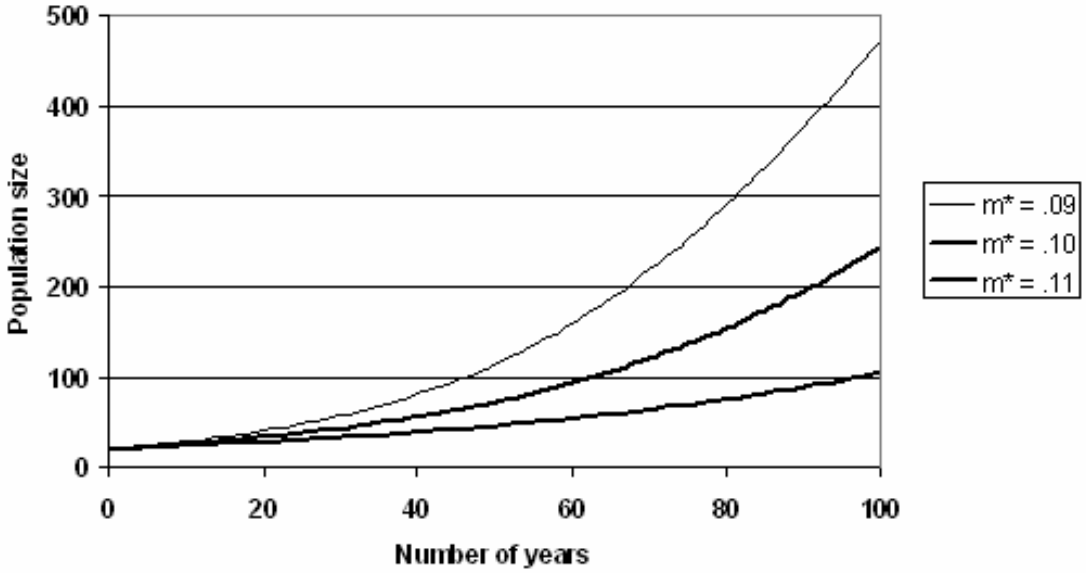

Figure 5. Effects on population growth when using the three alternative density dependent mortality rates of seals two years and older: $m^* = 0.11$, 0.10 and 0.09.

4. Sexual maturity, *f*

The portion of sexually mature individuals in a population reflects those that are able to reproduce. As follows, the age of attained sexual maturity may play an important role in the growth of a population. In our simulation the alternatives 4 and 5 years of sexually mature age shows two quite different growth rates (Figure 6). Density dependence in sexual maturity seems to have a profound effect only if the average age of seals giving birth for the first time decrease from the equilibrium value of 6 years to 4 years. Under these circumstances the initial population size of 20 individuals will become twice as large within 25 years, followed by an approximate doubling in size for every additional 25 year (Table 3).

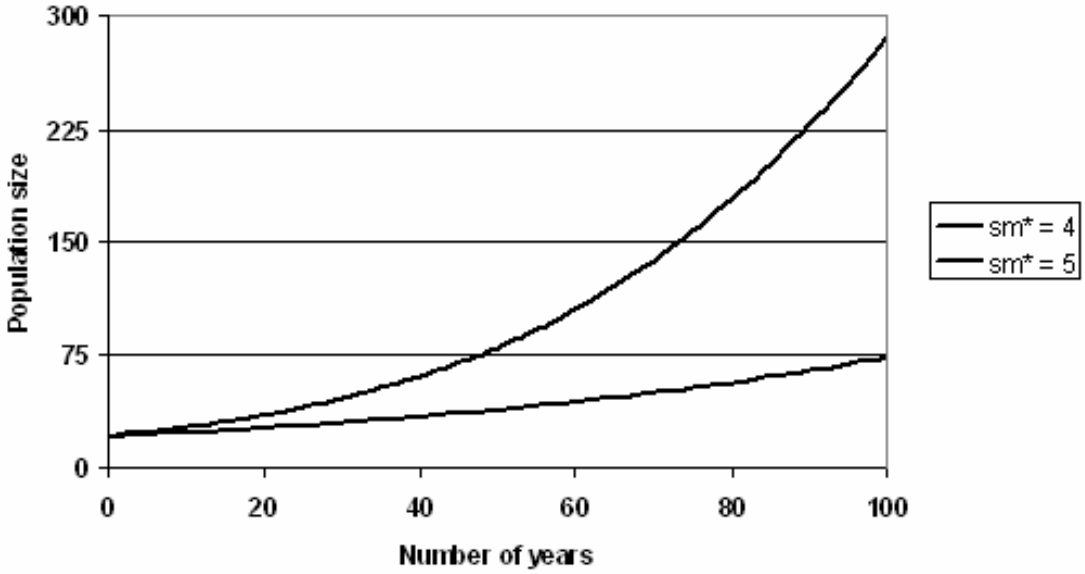

Figure 6. Effects on population growth when the age at sexual maturity drops from the equilibrium value of six years, to five and four years (i.e., sm*= 5 and 4 years). The two alternative ages correspond to $f_4^* = 0.40$, $f_5^* = 0.70$, $f_6^* = 0.90$, $f_7^* = 1$ and $f_4^* = f_5^* = f_6^* = f_7^* = 1$ respectively.

5. Fertility, *b*

When applying the alternative density dependent fertility rates $b^* = 0.85$, 0.90 and 0.95 in the population model, a noticeable increase may be observed (Figure 7). However, this increase has a relatively small influence on the overall population growth.
For instance, the maximal rise in fertility is from 80% to 95%, the population almost needs 50 years to become double its initial size (Table 3).

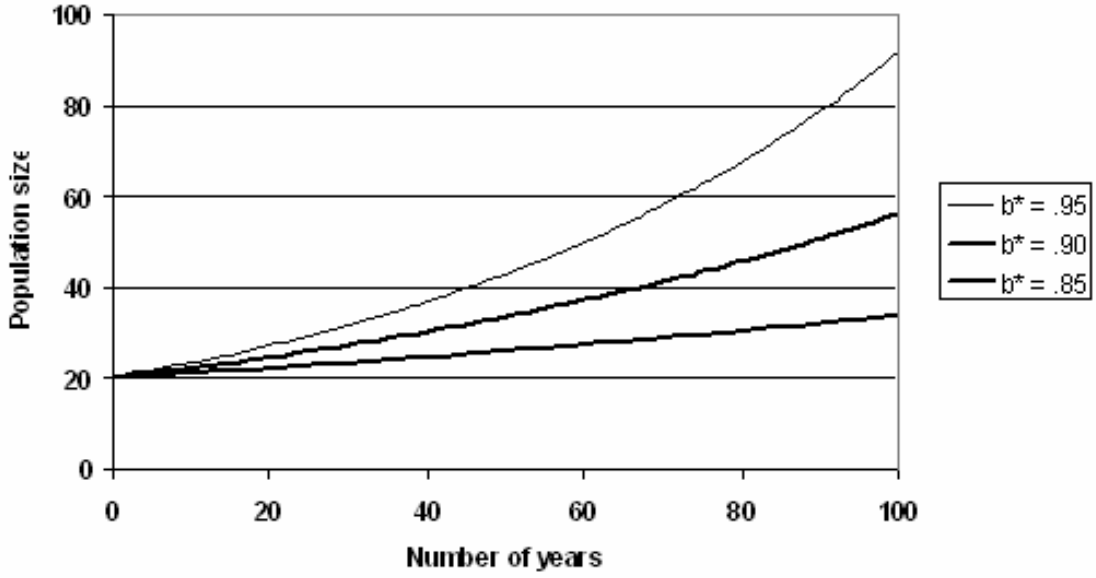

Figure 7. Effects on population growth when using the three alternative density dependent fertility rates: b* = 0.85, 0.90 and 0.95

Table 3. Numerical values of the population sizes after 25, 50, 75 and 100 years in the trajectories corresponding to various density dependent parameters that are natural mortality, sexual maturity and fertility (see text for further details). All simulations where started with an initial population size of 20 individuals.

	Natural mortality of pups'				Natural mortality in age group 1		Natural mortality in age group 2 and older		
Year	m_0*=. 30	m_0*=. 25	m_0*=. 20	m_0*=. 15	m_1*=. 15	m_1*=. 125	m*=. 11	m*=. 10	m*=. 09
25	28	33	38	44	26	27	30	38	48
50	40	55	74	99	33	38	46	72	114
75	57	92	144	216	42	52	69	137	253
100	81	153	263	408	55	71	105	244	472

	Age at sexual maturity		Fertility		
Year	sm*= 5	sm*= 4	b*=. 85	b*=. 90	b*=. 95
25	28	40	23	26	29
50	38	80	26	34	43
75	53	157	30	44	63
100	73	286	34	56	92

Approximations by the logistic growth model: age structure versus logistic

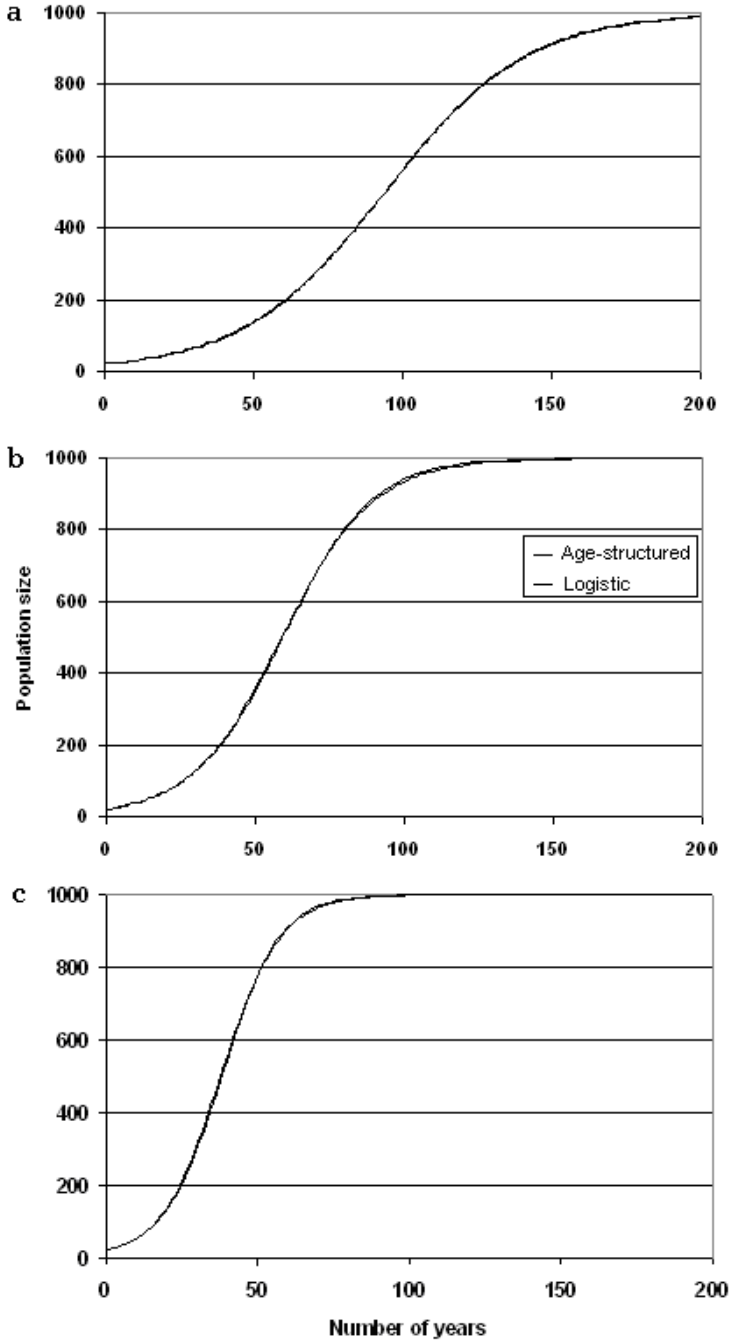

Figure 8. Population growth when applying an age specified model and an approximated logistic model. The logistic models are set with the intrinsic growth rates: r = (a) 0.042, (b) 0.067 and (c) 0. 105. The density dependent parameters in the age structured models are specified in the text. The two curves are practically identical giving the impression of only one curve present. See Appendix 1 for numerical values.

Figure 8 shows the characteristic sigmoid shaped curves that emerge in populations that are subjected to density dependent growth. Prior to approaching the carrying capacity, the population experiences an exponential increase, after which growth eventually is impeded.

The simulations where both models were employed under various growth regimes, illustrate two noticeable patterns. To begin with, the two growth models have merged into a single curve in each trial, making the two population trajectories almost indistinguishable. This demonstrates that the approximation of the logistic model to the age structured model is quite good. Secondly the convergence to the carrying capacity of a thousand seals is rather slow, even when applying a fast growth rate. Both the density dependent age structured

model and the logistic model share this property. For instance, given a slow growth rate (i.e. r = 0.042) the population barely reaches the equilibrium level within 200 years (Figure 8a). More importantly, at densities under 85% of the carrying capacity the population growth rate becomes so small that the time it takes to attain the equilibrium value is unrealistically long; 65 years to be exact. Similarly it takes nearly 30 years for the population to grow the remaining 15% of the equilibrium value when considering the fast growth rate (i.e. r = 0.105) (Figure 8c). Put in other words, our model population will have a very long recovery time even after a small perturbation removing 15% from the stable population size.

Overall, the population trajectories obtained with the logistic model showed remarkable approximations when comparing with the age structured model. It could therefore be appropriate to assess growth in a harbour seal population by means of the simpler logistic model. However, both models had an unrealistic long returning time towards the equilibrium, even when considering a small perturbation. Thus a constant growth rate was applied in the following simulations. For a detailed comparison of the numerical values, the trajectories representing the alternative density dependent growth models are listed in Appendix 1.

Simulations assessing dynamics and viability in a harbour seal metapopulation

Simulation 1: No emigration rate and random death of 5 (ER= 0 & RD= 5)

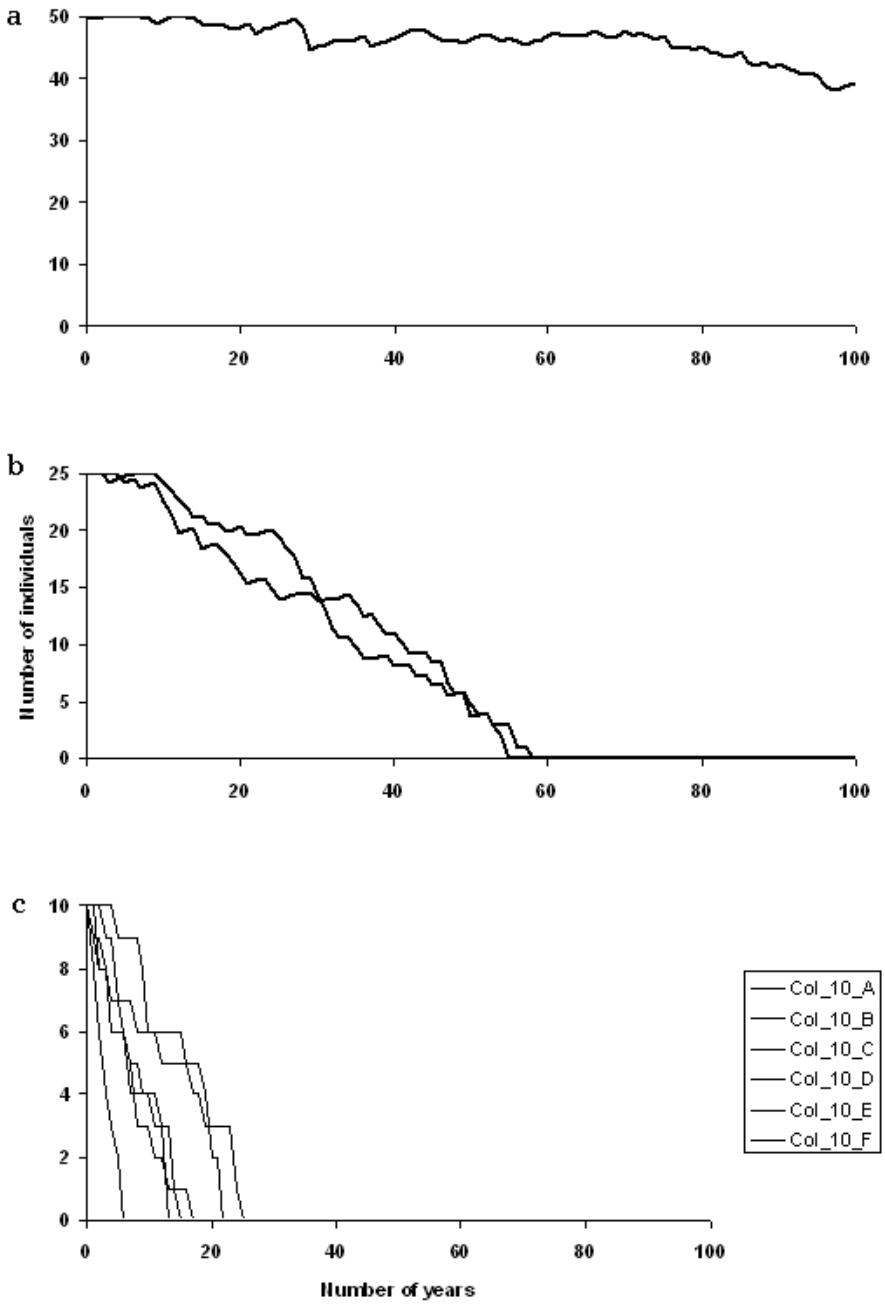

Figure 9. Effects on population sizes in the absence of emigration (ER= 0) from the main colony and with an annual random death rate of five harbour seals (RD = 5). The letters represent the different subpopulations with the following initial sizes: (a) 50, (b) 25 and (c) 10.

This simulation series illustrates what happens if the random death process is not balanced by recruitment from the main colony. All the satellite colonies fluctuate in size, but the evident decrease will eventually lead to extinction (Figure 9). In contrast, the main colony (not shown) stays constant at 400 individuals during the whole simulation period of 100 years (recall: not subject to random deaths). The initial size of the satellite colonies determines how fast they become extinct. For instance, the largest satellite colony with the initial population size of 50 seals will only lose 11 in the course of 100 years (Figure 9a); it almost lingers 200 years ahead (Appendix 1). The remaining smaller colonies with 25 and 10 seals disappear completely within 60 and 25 years, respectively (Figure 9b and c).

Simulation 2: Emigration rate of 0.02 and random death of 5 (ER= 0.02 & RD=5)

The second simulation demonstrates the outcome when the random mortality, applied in the prior simulation, is counteracted by recruitment from the main colony. Principally, the main colony and the three largest satellite colonies remain stable around their respective carrying capacities (Figure 10a). In sharp contrast, the six smallest colonies with an initial population size of 10 individuals undergo large fluctuations (Figure 10b).

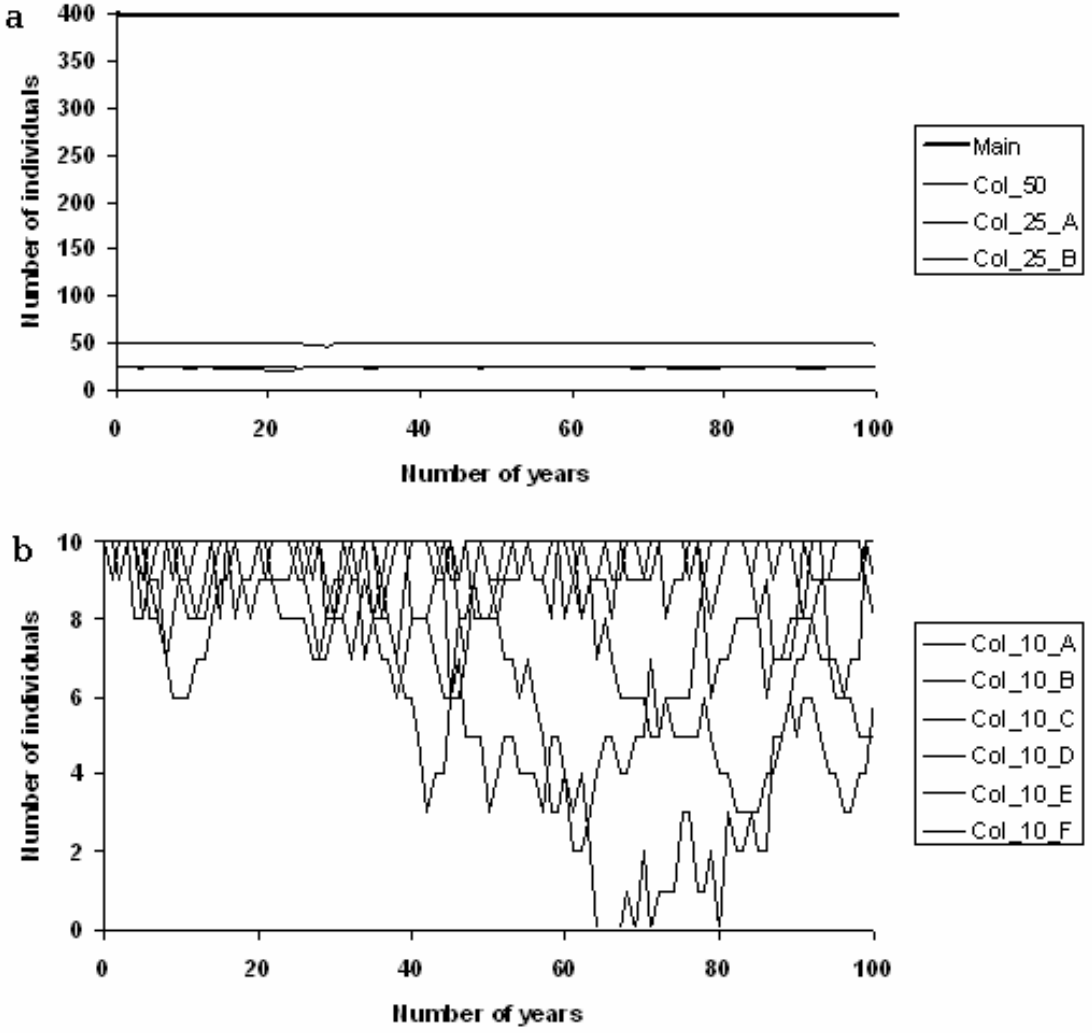

Figure 10. Effects on population sizes when emigration from the main colony is set to ER = 0.02, and the annual random death rate is set to RD = 5. The upper graph (a) represents the following colonies: the main with 400 individuals, one colony with 50 individuals and two colonies with 25 individuals. The lower graph (b) represents the remaining six colonies that have 10 individuals each. The initial sizes of the different colonies correspond to their carrying capacity (*K*).

When examining one of the smallest colonies more closely, one notices that it is vacant seven years in the period between the 64th and the 80th year (Figure 11 b_1). Even so, the colony manages to rebuild through immigration recruitment, to 5 individuals during the last 20 years.

Another colony with the same carrying capacity as the one described above illustrates the stochastic nature of small populations. Even though this colony also has an initial size of 10 seals, it never goes extinct during the 100 year period (Figure 11 b_2). By chance alone this colony will maintain 8 or more seals during 97 of the years.

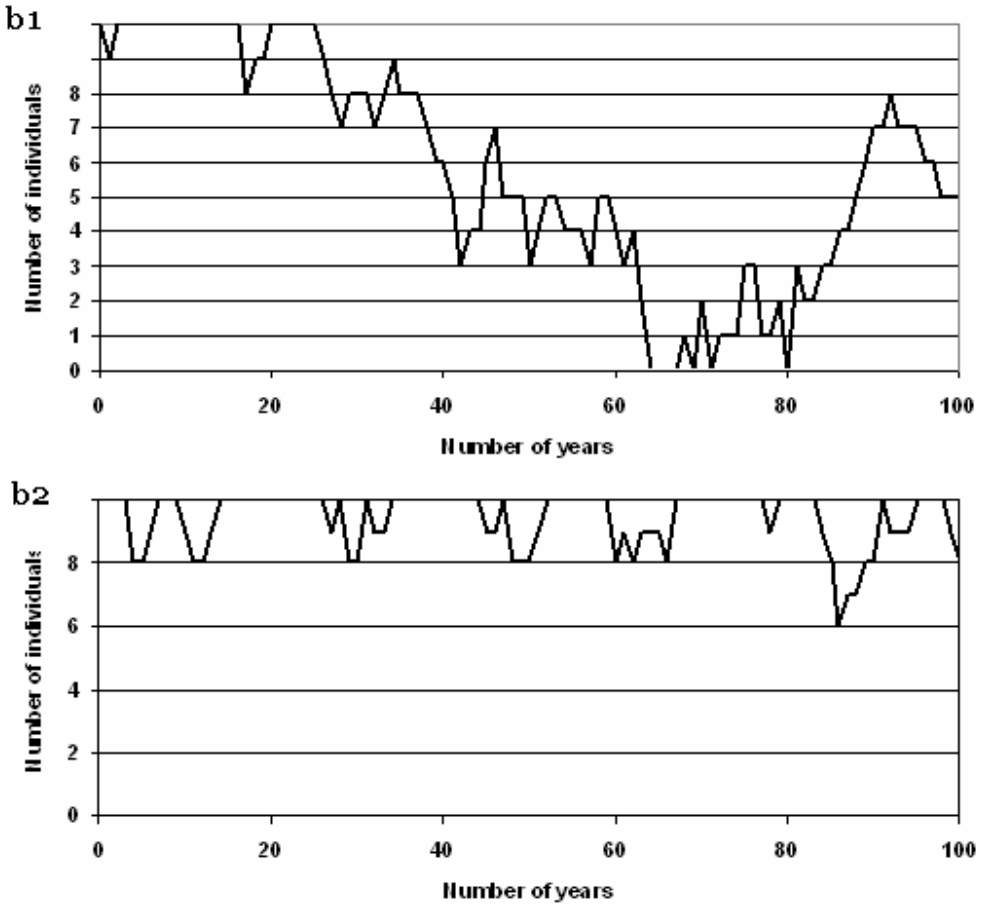

Figure 11. Effects on population sizes when emigration from the main colony is set to ER = 0.02, and the annual random death rate is set to RD = 5. Although both graphs, (b_1) and (b_2), represent colonies with an initial population size of 10 (i.e., their carrying capacity), they illustrate two quite different trends.

Simulation 3: Emigration rate of 0.02 and random death of 8 (ER= 0.02 & RD= 8)

The third simulation reflects how the population dynamics may develop when the process of random death is balanced by recruitment from the main colony (recall that the 2% emigration rate from the main colony corresponds to 8 recruits per year). Again it is seen that the main colony remains constant at 400 individuals. Although some minor fluctuations occur in the three largest satellite colonies, they still stay close to their equilibrium level (Figure 12a). Conversely, the six smallest colonies show an even more erratic behaviour than before (Figure 12b).

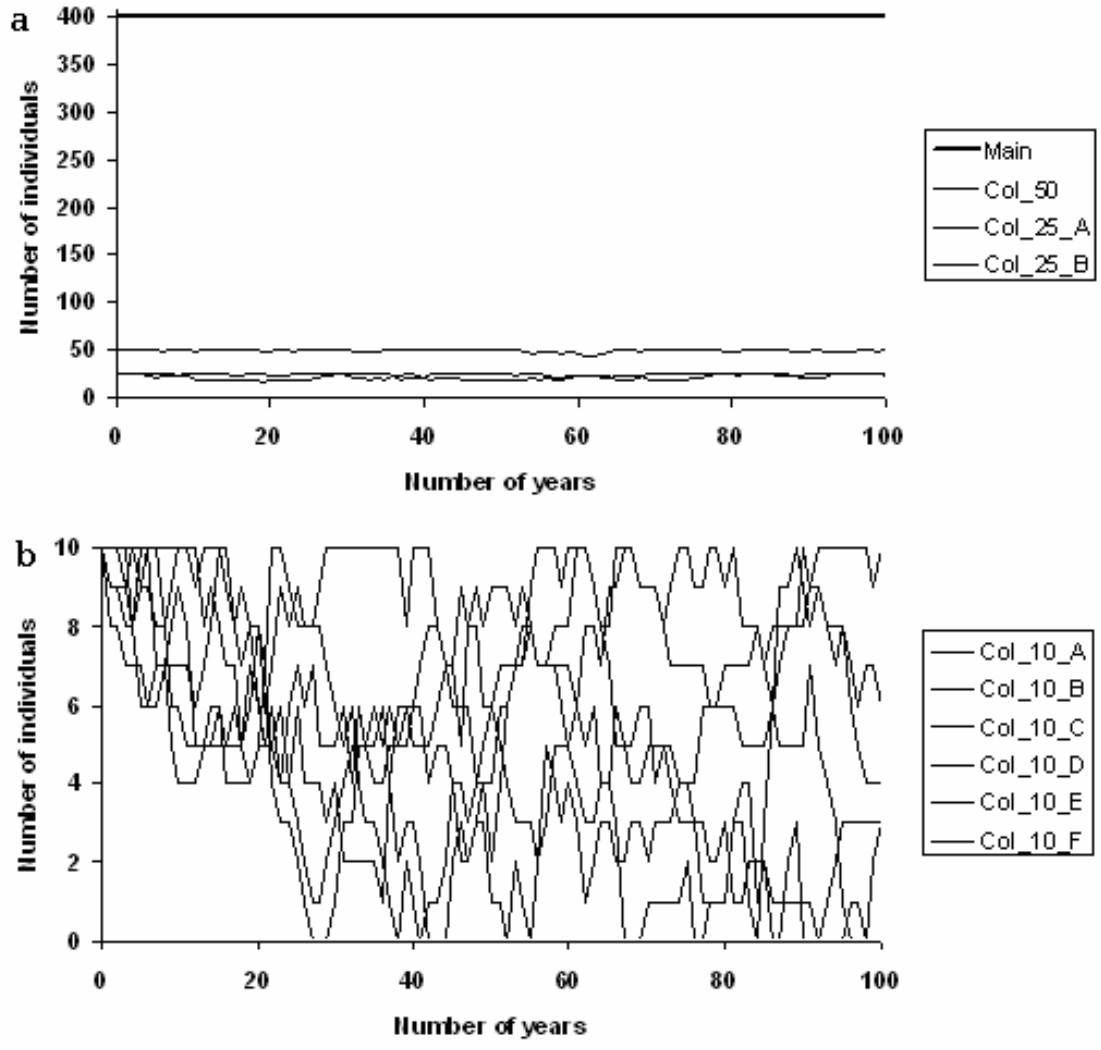

Figure 12. Effects on population sizes when emigration from the main colony is set to ER = 0.02, and the annual random death rate is set to RD = 8. The upper graph (a) represents the following colonies: the main with 400 individuals, one colony with 50 individuals and two colonies with 25 individuals. The lower graph (b) represents the remaining six colonies that have 10 individuals each. The initial sizes of the different colonies correspond to their carrying capacity (*K*).

Simulation 4: Emigration rate of 0.02 and random death of 12 (ER= 0.02 & RD= 12)

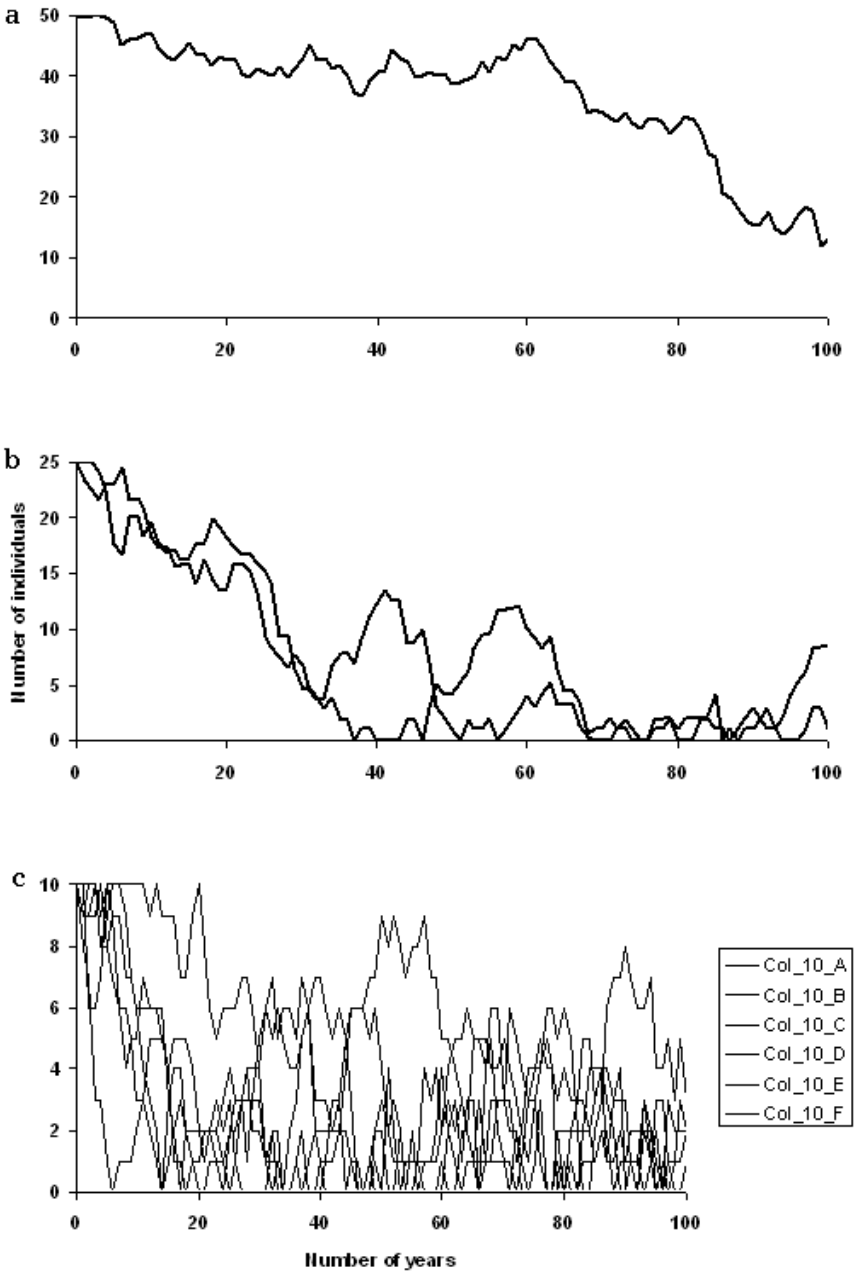

Figure 13. Effects on population sizes when emigration from the main colony is set to ER = 0.02, and the annual random death rate is set to RD = 12. The high mortality rate is thought to imitate the negative effects resulting from a long term environmental change. The letters represent the different subpopulations with the following initial sizes: (a) 50, (b) 25 and

What happens when the random mortalities exceeds the recruitment from the source population? In order to simulate the negative effects of a long term environmental change, the random mortality rate was set to 12%.

As usual the main colony stays constant at 400, but now the largest satellite colony with 50 seals declines substantially to an average of 16 seals the last five years (Figure 13a). The two colonies with 25 animals are reduced to relatively low levels past 40 years, after which they behave like the smallest stochastic colonies (Figure 13b). This is a consequence of the underlying assumptions of the population model.

Here the random mortality rates are larger than the combined effect of inner recruitment (1%) and recruitment through immigration from the main colony. As a result, all the large satellite colonies will be reduced to a population level where recruitment essentially is provided by the random immigration. This is especially a characteristic of the dynamics regulating the six smallest colonies. As expected, these six colonies experience more and more violent fluctuations as the random death rates increase (Figure 13c).

Simulation 5: Rebuilding after a catastrophic event: r = 0.05, ER= 0.02 & RD= 0

The purpose of the subsequent simulation series was to explore the recovery times after a supposed catastrophe had struck our harbour seal metapopulations. As previously described, all colonies are thought to vanish after such an event except for the main colony which is left with 100 seals. Further it was assumed that an elevated intrinsic growth rate (i.e. a 5% increase) in the rebuilding phase of the main colony, while the emigration rate continues as before (i.e. 2%).

The first simulation attempts to assess the effects of the stochastic death process, so the mortality rate is set to zero in this trial. The regrowth of the main colony and the satellites expectedly comes about in varying tempos (Figure 14). Initially, the six smallest colonies attain their equilibrium value of 10 individuals in 35 years on average (Figure 14b). The main colony, on the other hand, is re-established after 45 years, closely followed by the two colonies with 25 seals recovering within 50 years (Figure 14a). At last the largest satellite colony reaches its equilibrium value of 50 individuals after 65 years.

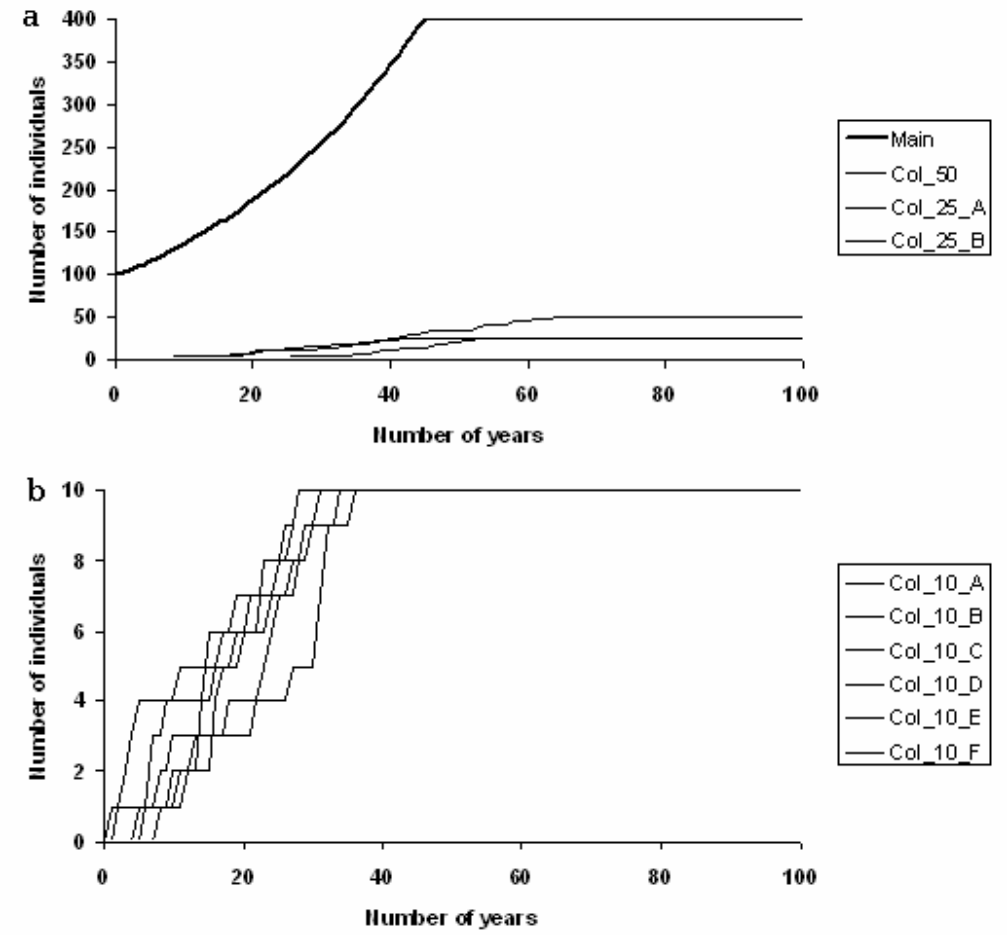

Figure 14. Effects on population size when catastrophic event occurs. The catastrophe wipes out all the colonies except the main one, where a hundred harbour seals are left. It is assumed an elevated intrinsic growth rate of r = 0.05 in the main colony, but the emigration rate is maintained at ER = 0.02. No random deaths is assumed, giving RD = 0. The upper graph (a) represents the main colony and the subsequent three colonies, where the carrying capacities are 400, 50 and 25 seals respectively. The lower graph (b) represents the remaining six smallest colonies with an equilibrium size of 10 individuals.

It should be noted that the population trajectory of the main colony will be the same for any given value of random death, which will be applied in the last two simulations. This is, as we have been observing in our previous simulations, due to the fact that the population dynamics of the main colony is independent of those in the satellite colonies. Thus the main colony has not been considered in the next trials.

Simulation 6: Rebuilding after a catastrophic event: r = 0.05, ER= 0.02 & RD= 3

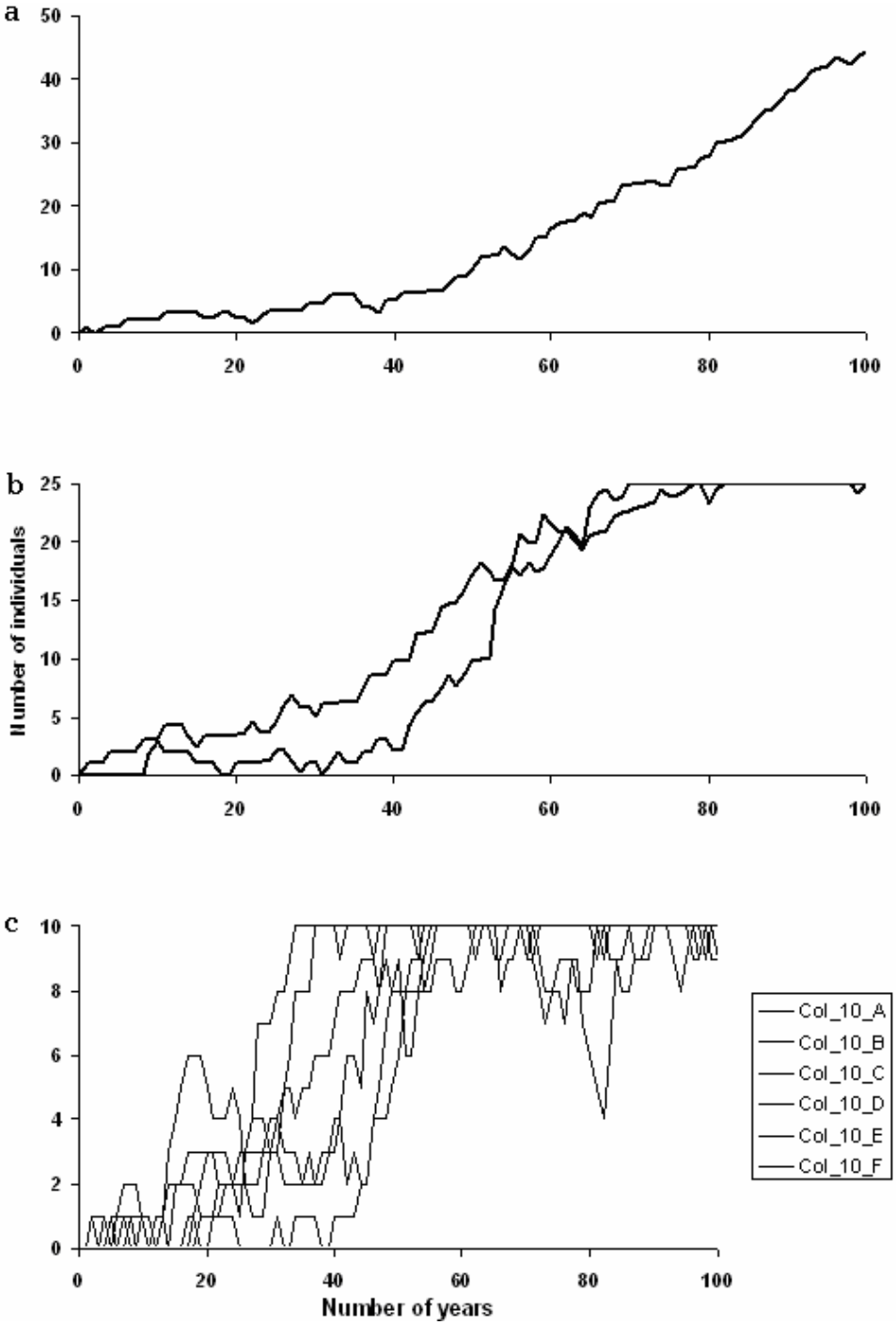

Figure 15. Effects on population size when a catastrophic event occurs. It is assumed an elevated intrinsic growth rate of r = 0.05 in the main colony, and the emigration rate is maintained at ER = 0.02. Random deaths are set to RD = 3, which is not applied to he main colony. The letters represent the different subpopulations with the following carrying capacities: (a) 50, (b) 25 and (c) 10.

When applying a random death rate of only 3 seals per year, the stable population abundances are restored noticeably later compared to when death rates are absent. After 100 years the largest satellite colony has not yet reached the equilibrium level of 50 seals, but rather has 43 at this point (Figure 15a). The two colonies with the carrying capacity of 25 seals, on the other hand, are re-established within 80 years (Figure 15b). Finally, the six smallest colonies with a carrying capacity of 10 animals will on average rebuild after 60 years, although they show some oscillations (Figure 15c).

Simulation 7: Rebuilding after a catastrophic event: r = 0.05, ER= 0.02 & RD= 8

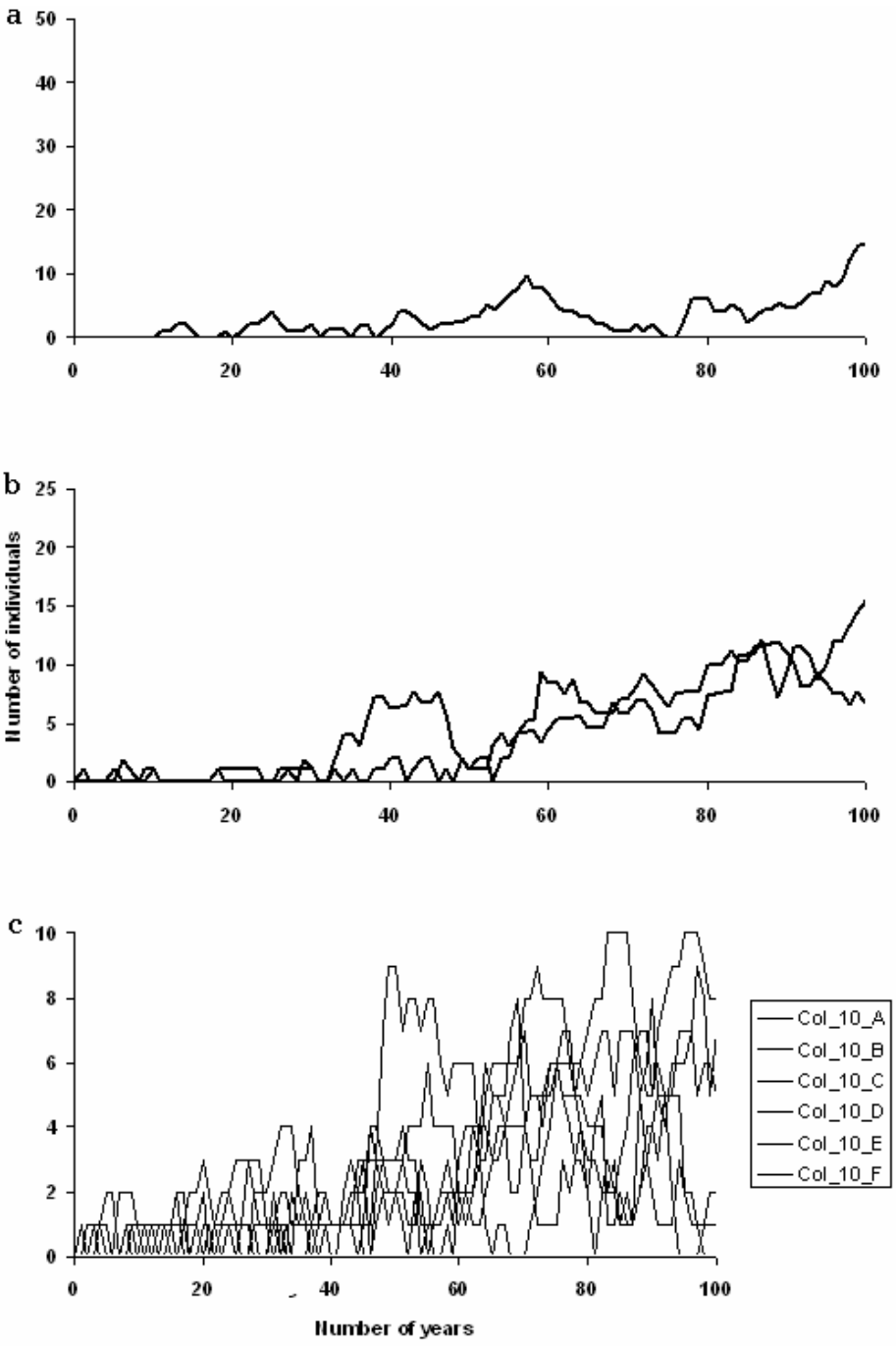

Figure 16. Effects on population size when a catastrophic event occurs. It is assumed an elevated intrinsic growth rate of r = 0.05 in the main colony, and the emigration rate is maintained at ER = 0.02. Random deaths are set to RD = 8, which is not applied to he main colony. The letters represent the different subpopulations with the following carrying capacities: (a) 50, (b) 25 and (c) 10.

In the final simulation, the random death rates are balanced by recruitment from the main colony.

As anticipated, the level of stochastic mortality rates effectively impedes the process of rebuilding. Turnover events are not only restricted to the smallest satellite colonies, but are also seen in the larger ones. In the course of 100 years the population level has only reached an average value of 12 seals in the largest satellite colony (i.e. K = 50) (Figure 16a). Similarly, the colonies with a carrying capacity of 25 seals barely consist of more than 10 individuals, on average, within the same period (Figure 16b). Despite showing an upward trend, the six remaining colonies have highly unpredictable fluctuations that lead to a mean of 4 seals per colony by the 60th year (Figure 16c).

DISCUSSION

Sensitivity analysis of the parameters

Of the five density dependent parameters examined, age at sexual maturity together with natural mortality of pups and in seals older than two years proved to have the greatest effect on population growth. The population model suggests that these parameters significantly regulate the growth rate of harbour seal colonies.

The survival of pups is an obvious criterion for population growth. Apart from possible contribution through immigrating seals, pups represent the main income of individuals. This is correlated with natality (realized fertility rate). The age at sexual maturity, which in our simulation represent the age at first reproduction, is further linked to the pup production. The sooner an individual becomes mature, the faster it can contribute to the population growth. In addition, the survival of seals two year old and older will have a significant effect on the increase of a colony. The majority of these animals constitute the reproductively capable fraction of the population. Therefore, if mortality is high, fewer individuals are able to contribute to the population growth.

Approximations by the logistic growth model

The approximation of the logistic growth model to the age structured model turned out to be quite good. Although the age structured model included age-specific parameter values, the two trajectories still were practically indistinguishable. An apparent advantage that the logistic growth model offers is that one does not have to consider neither age- nor sex-specific demographic parameters. The reason why the approximation is so successful is essentially linked by the relatively fixed relationship between newborn pups and the number of sexually mature females. When the age structure is more or less in accordance with the age dependent natural mortalities (Table 2), the number of sexually mature females will comprise a certain fraction of the total population. Both models, however, had an unrealistically slow convergence towards the equilibrium level (i. e., carrying capacity). Thus a constant growth rate was applied in the succeeding simulations.

There have been attempts to modify the speed at which the population approaches its carrying capacity. Density dependent population growth is therefore commonly represented by a generalized logistic model (Pella and Tomlinson 1969) which incorporates a shaping parameter (z). When z >1, the population approaches its carrying capacity faster than a logistic model would predict, while the opposite is true when z < 1. This model has, among others, been applied to harbour seal populations and seem to describe the demographic trends better when z >1 (Jeffries *et al.* 2003).

Simulations assessing dynamics & viability in a harbour seal metapopulation

The initial population models used in this study represent a closed system where neither immigration nor emigration is considered, leading the population size to be driven solely by births and deaths. In order to assess a more realistic setting, a hypothetical harbour seal metapopulation was modelled by adding both migration and stochastic events.

Source-sink dynamics

The observed results demonstrated a fundamental feature in the source-sink dynamics of metapopulations. The dynamics of the source or core colony was independent of that of the sinks (i.e. "self-supporting"), while the opposite was true for the nine sink colonies. The initial size of the various satellite colonies did affect this relationship to an extent, for example in terms of the time it took before a colony died out. Another prominent feature that was noticed is that a stable colony structure (i.e. at the specified carrying capacity) could only be maintained if the random death did not exceed the recruitment from the main colony. This implies that in the sink habitats, the output of juveniles or adults to the breeding stock was not sufficient to balance mortality.

Stability

When it comes to the stability of the different colonies, it appeared quite clear that smaller colonies were less stable. Since the main colony was not subjected to random mortality, it remained fixed at 400 individuals throughout the trials when applying various stochastic death rates (i.e., RD = 5, 8 and 12). The largest satellite colonies, however, consisting of 50 and 25 individuals, remained more or less at their respective equilibrium values as long as the random death rate was lower than the recruitment from

the core colony. In sharp contrast, the six remaining satellite colonies showed a highly unstable behaviour. With only 10 individuals and no inner recruitment, the colonies relied completely on the randomly provided immigration recruitment to survive. Accordingly, as the random mortality rates increased, these small colonies subsequently experienced more and more violent and erratic fluctuations.

The stochastic nature of small populations was also demonstrated by the fact that the fate of the smallest colonies was not necessarily extinction. Even though one colony of ten seals could experience four extinctions and subsequent rebuilding in the course of 100 years, another equally sized colony could persist without a single extinction event. The on and off existence of some of these colonies illustrates the turnover events (i.e., local extinctions and establishment of new populations) that metapopulations might experience.

Migration

Population size is significantly affected by migration, and is regarded as a central aspect of metapopulation dynamics. As pointed out earlier, all the satellite colonies were in varying degree dependent on the recruitment from the main colony. Without any provided immigration, all the satellites gradually became extinct, which is a characterizing feature of sink populations. Again the size of the colony, at least partly, determines how reliant it is to the income of dispersers. An additional aspect is that the three largest satellite colonies were also given inner recruitment, which to some level limits this dependence of immigrating seals. In this manner, stability is enhanced and an eventual extinction may be postponed.

As expected, the simulations also showed that random mortality had a greater effect on the colonies having the smallest congregation of animals. At elevated death rates the reproduction or recruitment was at insufficient levels to balance the mortality. The only way the sink or satellite colonies could be maintained was through dispersal from the productive source colony.

Population recovery after a catastrophic event

When our harbour seal population was subjected to a supposed catastrophic event, the simulations once more demonstrated the vulnerability of the small colonies. With an absent mortality during the rebuilding process, all colonies recovered and reached their equilibrium size well within 100 years. However, in the presence of stochastic mortality the population growth was effectively impeded in all the sink habitats. When additionally elevating the death rates to equalise the immigration recruitment, the unpredictable behaviour of even the biggest satellite colony resembled that of the smallest. All the satellites were subjected to turnover events and thus displayed stochastically (i.e. highly unstable).

Reassessing the results to real harbour seal populations

Now that the results have been summarized, several questions arise: How may the distribution of local populations be explained and what kind of role does migration play? How does density dependence display in demographic parameters and thereby in growth within natural harbour seal populations? What kind of impacts could major catastrophic events have on population dynamics associated with the rebuilding process? How applicable are our results to real pinniped populations? These and other aspects of population dynamics will be considered in the following section.

Size, distribution and dispersal

The Northeast Atlantic harbour seal (*Phoca vitulina vitulina*), is distributed over a wide range of habitats and ecosystems and the size of the various populations differ greatly, both locally and regionally (Härkönen 1987b). In order to explain the pattern of distribution and abundance of harbour seal colonies, different aspects of habitat suitability and dispersal need to be considered.

Reviewing the factors that are known to limit the abundance of marine mammals, Harwood and Rohani (1996) found that the most important factors were the availability of safe areas to breed and forage. Pinnipeds in general require specific habitats for breeding on land, but at the same time they are constrained by foraging at sea, therefore

selection of breeding areas becomes crucial. Several studies have revealed that movements between haul-out locations and feeding grounds usually are between a distance of 50-70 km (Thompson *et al.* 1989; Thompson and Miller 1990; Thompson *et al.* 1991; Bjørge *et al.* 1995; Thompson *et al.* 1996; Bjørge *et al.* 2002). In addition, they utilize specific resting sites that they remain faithful to year after year, although the importance of different haul-out areas may vary seasonally in response to migrating fish and other abundant food supplies (Thompson *et al.* 1996).

Considering all these features, it becomes clear that a typical habitat should provide suitable haul-out sites that offer refuges during parturition and lactation and have sufficiently food in close proximity to sustain the population throughout the year (Bjørge et al. 1993). Thus, distribution may be interpreted by the presence of such habitats (Bjørge *et al.* 1993). In fact, this seems to partially explain the local and regional distribution of harbour seals in the Skagerrak (Härkönen and Heide-Jørgensen 1991). However, it is often seen that apparently suitable and readily accessible breeding sites sometimes are unoccupied. One explanation for this might lie in the behaviour of the seals themselves. Several studies have revealed explicit site fidelity (i.e. philopatry) in harbour seals (Härkönen *et al.* 1999; Härkönen and Harding 2001; Härkönen 1987). It has been suggested that strong site fidelity may help to explain observed heterogeneities in distribution, and that it to some extent may increase isolation between colonies (Matthiopoulos *et al.* 2005).

When comparing the harbour seals resident in the Skagerrak and Kattegat, twice the number of seals has been counted in the Kattegat (Table 1). However, the distribution of seals and the colony sizes in the area show little variation from year to year (disregarding former hunting periods and epidemic events). The same kind of stability of colony sizes was also emphasised by Øynes (1966) along the coast of Southern Norway in the 1960s. Øynes (1966) reported that most colonies held between 10-20 animals, and that the number of seals residing along the coastline from Vest-Agder to Vestfold was stable at the regular haul-outs.

Migration

Even though harbour seals primarily are considered to be sedentary, numerous studies have shown that they are capable of wide dispersal (Bonner and Witthames 1974; Wipper 1975; Pitcher and McAllister 1981; Reijnders *et al.* 1982; Wiig and Øien 1988; Thompson *et al.* 1989; Bjørge *et al.* 2002). Tagging and telemetry studies suggest that adult seals are strongly philopatric with only locally restricted movements, while pups account for the majority of migrations observed in harbour seal populations. These young animals are capable of travelling long distances in short periods of time, with around 20% of the individuals undertaking long distance movements of up to 500 km (Wiig and Øien 1988; Thompson *et al.* 1994). Studies have indicated that harbour seals do not make extensive migrations before three months subsequent to weaning (Wipper 1975; Drescher 1979) and it seems that the pups disperse in random directions from their natal sites (Summers and Mountford 1975; Wipper 1975; Vaughan 1978). A study conducted at the Koster Island on the Swedish west coast showed that nearly 25% of the branded pups had migrated to other colonies during their first year (Härkönen 1987a). During the second and third year, most of the cohort appeared to reside in the area where they were born.

It has been suggested that through dispersal, species are able to self-regulate their population size and reach an equilibrium with their environment (Chitty 1960), and studies have demonstrated that migration between fragments greatly reduces the probability of extinction (Goodman 1987; Burkey 1989).

A model for the uneven distribution of harbour seals

Despite the fact that harbour seals have been documented to migrate extensively between colonies, seal groups still exhibit an uneven distribution on a local scale. However, one would rather expect the abundance of the colonies to converge in size, as a result of random migration, than having the differences maintained. This local unevenness cannot be caused by the lack of haul-out places, since only a small portion of available sites are utilized even in densely populated areas (Härkönen 1987b). Owing to this paradox, Härkönen (1987b) proposed a theory in order to explain the phenomenon by pointing out that the ecologically effective feeding grounds are considerably shallower than indicated

by the maximum diving capacity of the species (450 m) (Folkens and Reeves 2002). Even in areas where deep bottoms are available, the documented feeding depths are less than 30 m (Härkönen 1987b; 1988; Bjørge *et al.* 1995). Härkönen further emphasised that the abundance of prey depends on depth and the local geography of the sea bed, and thereby limits the available hunting grounds. That is why the size of the feeding areas, depending on local bathymetrical conditions, may have a significant influence on colony size. Furthermore, the variety of foraging habitats utilized by the harbour seals, and the manner in which they tend to return to the same feeding sites, may indicate individual specialization to avoid intraspecific competition.

Demography and population growth rate

For any population there is an upper rate of increase. In harbour seals the single annual offspring along with the age at first parturition poses two important limitations for population growth (Härkönen *et al.* 2002). In addition to these physiological constraints, density dependence acts as another regulating mechanism.
Several studies have shown that pinniped populations are density dependent, seemingly a general pattern among large mammal species (Fowler 1981a). Species such as the harbour seal, showing low reproductive rates, late maturation, long life spans and having resource limited populations (often referred to as the K-selected species), in general experience that the majority of density dependent changes in vital rates occur close to the carrying capacity (Fowler 1981b).

Our result demonstrated how alterations in mortality and age at sexual maturation induce significant changes in population growth. In a study of grey seals (*Halichoerus grypus*) in Britain, (Harwood and Prime 1978) showed that the population dynamics were less sensitive to fluctuations in fertility than to variations in mortality, especially in adult seals. In particular, altered demographic parameters and subsequent growth rates have been observed at lowered population sizes often as a result of exploitation (Bowen *et al.* 1981; Eberhardt 1981; Lett *et al.* 1981; Heide-Jørgensen and Härkönen 1988). Changes in age at sexual maturity in response to hunting pressure have been documented in several seal populations (Bigg 1969; Boulva and McLaren 1979; Bowen *et al.* 1981), and

at low population densities, it is assumed that more food resources become available. Hence, individual consumption and growth rate (i.e., body weight) increases and sexual maturation may occur earlier. According to Bowen *et al*. (1981) the age of maturity in harp seals (*Pagophilus groenlandicus*) had decreased from six years to four years during the past thirty years. This change was thought to be influenced by exploitation and reduced population size. Similarly, larger reproductive potential have been observed in heavily hunted populations of harbour seals in British Columbia (Bigg 1969) and eastern Canada (Boulva and McLaren 1979). Compared to unexploited populations, these displayed early ages of maturity and high pregnancy rates.

Environmental stochasticity

Seeing that density dependent factors act most strongly on dense populations, the growth potential of a population is least restricted when its numbers are small. Under such circumstances it also faces the greatest probability of extinction by random events.

In our attempt to predict the outcome of stochasticity, our population model, consisting of variously sized colonies, was roughly based on the observations reported by Øynes (1966) in Southern Norway. From the simulations it was found that an equilibrium distribution of seals was established when the random death process in the colonies was balanced by emigration from the main colony. Under these circumstances the main colony remained constant at 400 and the colonies with abundances of 50 and 25 individuals stayed close to their equilibrium level (Figure 12a). Quite the opposite behaviour could be observed in the remainder of the smallest colonies that, with a carrying capacity of only 10 animals, suffered from violent fluctuations (Figure 12b). These simulations therefore indicate that in a stochastic environment, colony sizes above some critical level close to 20 animals will stabilize, and according to the classification of Øynes (1966): “remain constant from year to year”. However, the small colonies, like those in the inner Oslofjord, will fluctuate around some long-term level of 5 seals.

Hence, as a first approximation the simulations seem to be realistic. They further suggest that when the expected emigration to each satellite colony is equal to the expected

mortality, the colony abundances will rather stabilise than equalise in the long run. In fact, several studies have documented the skewed distribution of harbour seals within its ranges (Øynes 1966; Bonner and Whitthames 1974; Härkönen 1987b).

Population declines in Skagerrak and Kattegat

As pointed out earlier, high growth rates are often associated with depleted populations. Aerial surveys conducted in Kattegat-Skagerrak during the years 1979-1986 indicated an annual rate of increase of 0.11 in the harbour seal population (Heide-Jørgensen and Härkönen 1988). Prior to being protected in 1967 and 1977 in Sweden and Denmark, respectively, hunting had seriously reduced the abundance of seals. The high increase was assigned to be a density dependent response. Growth rates of similar magnitude have only been recorded in pinniped populations that have been recovering after a period of overexploitation. An example is the Antarctic fur seal (*Arctocephalus gazella*) which due to hunting in the 19th century showed a population growth rate of 16.8% (Bonner 1982). Such high growth rates may be an indicator of an unstable pinniped population; seal populations in general tend to increase at rates well below 10% (Payne 1977; Harwood 1981). It has been suggested that the high growth rate may have coincided with the reduction of other species, which compete with the harbour seal for food resources, such as the grey seal (*Halichoerus grypus*) and the harbour porpoises (*Phocoena phocoena*) (Andersen 1976). Accordingly, reduced interspecific competition may have contributed to the observed increase (Heide-Jørgensen and Härkönen 1988).

In contrast to the relatively high growth rates of the Kattegat-Skagerrak stock mentioned above, the ones applied in our simulations could therefore be regarded as conservative. Compared to other well-studied populations, a choice of 5% seems realistic when the abundance is over ¼ of the carrying capacity. Given the lack of information concerning the population growth in Norwegian harbour seals, the chosen growth rate of 5% was used when studying the effect of severe perturbations.

Population recovery after catastrophes

Environmental stochasticity may sometimes manifest itself as a catastrophic event, wiping out large proportions of a population in a very short period of time. One such

event has been the outbreak of the phocine distemper virus (PDV), also known as "the seal plague". In 1988 European harbour seals were affected by what was described as the worst epizootic ever recorded for pinnipeds. More than 23 000 harbour seals were killed across Europe by the previously undescribed morbili virus (Dietz *et al.* 1989; Härkönen *et al.* 2006). Prior to the 1988 outbreak, the Kattegat-Skagerrak stock had increased at an exponential rate of more than 10%, and numbered a total of approximately 9100 animals (Heide-Jørgensen and Härkönen 1988). The virus killed at least 5400 seals in Swedish and Danish waters of Kattegat and Skagerrak, and the total mortality was estimated at 60% where no differences were found between sub areas (Härkönen and Heide-Jørgensen 1990). The largest colony in the Norwegian Skagerrak, Hvaler (Østfold), suffered a decline of 75% (Markussen 1992).

In 2002, a second outbreak ravaged the European harbour seal populations, this time causing a 66% reduction in the northern parts of Skagerrak (Härkönen *et al.* 2006). Harding *et al.* (2002) showed that if the epidemic outbreaks occur at 14 year intervals and less than 80% of the animals die, then the populations have a reasonable chance to recover. If, however, the reoccurrence of such an event is more frequent, the outcome may be fatal.

In our simulation the supposed catastrophic event caused approximately 80% mortality in the population as a whole. As previously explained the rate of growth in the main colony was set to 5% due to the density dependent effects associated with lowered population abundance. Assuming no stochastic death process the average return time was in the order of 50 years (Figure 14). When the stochastic death process was set to balance out the recruitment by immigration from the main colony, the rebuilding process of the satellite colonies was severely obstructed (Figure 16).

It is difficult to extrapolate our results and apply them to a specific or concrete event in the Norwegian harbour seal population. The 45 years required to re-establish the main colony was crucially dependent of the given 5% growth rate. If the true growth rate is much higher, for example as reported in the Kattegat-Skagerrak between the 1970s and

1980s (Härkönen and Heide-Jørgensen 1990), the recovery time will rather be around 20 years. When considering the re-growth of the satellite colonies, it becomes clear that it heavily depends on environmental stochasticity. When the random death process is equalised by emigration, the satellite colonies may need more than twice the time to reach the carrying capacity when compared to the source colony. However, in order to make more precise estimates, observations on population growth rates along the Norwegian coast are needed.

Despite anthropogenic interferences and recurrent epidemics, the harbour seals in the Skagerrak and Kattegat have shown a remarkable ability to recover (Figure 17). The rate of recovery of a seal population will depend on the segments of the population that are killed. It is easy to imagine that the loss of a year's offspring is more rapidly compensated than is equivalent loss of adults. By ensuring adult survival, particularly in females, long term persistence may be attained in a population. Reviewing factors that may influence pinniped population recovery, McLaren (1990) argued that populations close to equilibrium should show less enhanced growth rates following a substantial reduction in numbers than those well below.

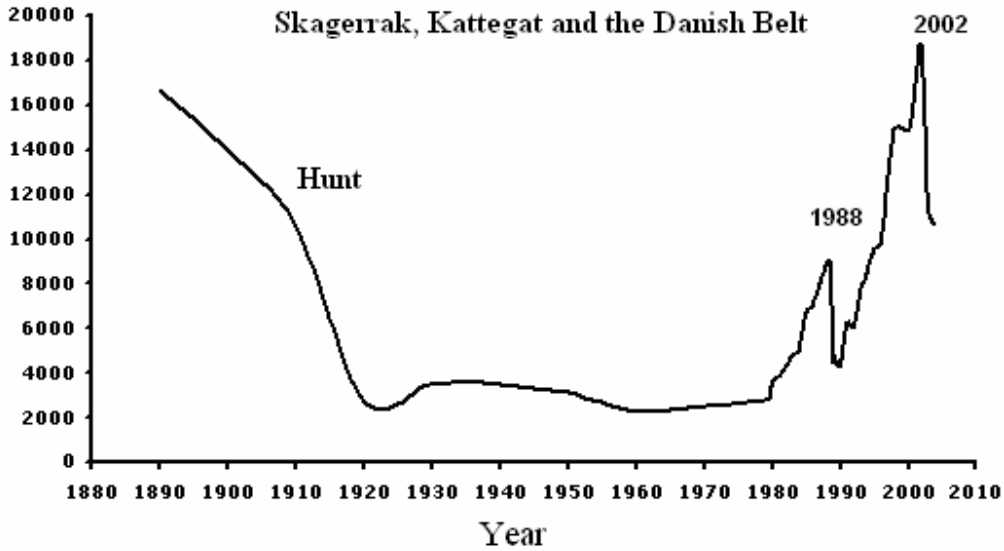

Figure 17. Times series showing the overall population trend in harbour seals between the years 1890 and 2004 in Skagerrak, Kattegat and the Danish Belt. The numbers are based on hunting statistics (1890-1977) and aerial surveys (1979-2004)(Härkönen 2006).

Status of the local harbour seal populations along the Norwegian Skagerrak

At present there are a few harbour seal colonies scattered along the coast of the Norwegian Skagerrak. Unfortunately, the current fragmented distribution may primarily be assigned to the conflicts that have come to pass between man and seal, especially in the 19th and the beginning of the 20th Century (Øynes 1966; Bjørge 1993; Henriksen and Røv 2004). The harbour seal was, and still is, perceived as a competitor for fish and blamed for causing damage to fishing equipment. Being branded as vermin, the populations were severely decimated and even today, harbour seals are rare in Southern Norway (Bjørge *et al.* 1994). As recently as the 1980's, a culling program was carried out in the Skagerrak to reduce the coastal seal populations, despite being legislatively protected in 1973 (Bjørge *et al.* 1994). A more recent and rational concern that has triggered new conflicts has been the dispersal of parasitic nematodes from seals to fish, where infestation of commercially important fish causes significant economic losses (Bjørge *et al.* 1981; Bjørge 1996; Henriksen and Røv 2004). However, there is not an unambiguous relationship between the size of the seal population and parasite load in fish (Andersen *et al.* 1995).

Like most other coastal areas, the Kattegat-Skagerrak waters are in close vicinity to urban settlements and human activities accompanied with it (e.g. boat trafficking and pollution), potentially disturbing seal colonies residing nearby. It should not be ruled out that this could make some areas unsuitable for harbour seal settlement, and partly explain the limited harbour seal abundances seen in parts of Skagerrak. In some areas, however, the seals probably have habituated to human activity.

The fragmented harbour seal colonies along the Norwegian Skagerrak are most likely sustained through dispersal. The relatively large seal colony at the Hvaler archipelago (Østfold), undoubtedly serves as an important source of recruitment to other local subpopulations in the outer Oslo fjord and along the Norwegian Skagerrak (Ugland *et al.* 1984). Nevertheless, the neighbouring Koster archipelago being the largest seal colony in the Skagerrak, could contribute through dispersing animals. In fact, it is generally

believed that the two colonies are part of a larger population with two separate breeding areas (Ugland *et al.* 1984).

Although migration among the colonies may buffer against local extinctions, the limited size of the local subpopulations still proposes an uncertain prospect if exposed to severe catastrophic events. The unpredictability of an oil spill or an epidemic outbreak makes it especially important to prevent other anthropogenic induced mortalities, such as hunting, drowning in fishing nets or habitat deterioration. Stochastic events should therefore be taken into consideration when managing harbour seals populations. Protection of, in particular, source areas such as at the Hvaler archipelago may perhaps ensure long-term persistence of the small local populations. This being said, the harbour seal colonies have remained in spite of repeated threats from epizootic outbreaks and human interference. There are no studies, to my knowledge, that have explicitly described the migration rate between the colonies in Southern Norway. In order to assess the dynamics and thereby viability of these colonies, it would have been interesting to obtain a more detailed picture of such movements.

CONCLUSION

All things considered, stochastic events may have significant impacts on long-term population growth and viability. Since such random events do not discriminate between sex and reproductive status of individuals, they may impose the biggest threat when populations are small or fragmented. Whether by reasons of mass mortalities or other events causing vital changes in abundance, the community structure may be altered and ultimately influence long term population dynamics (Harwood and Hall 1990). According to McLaren (1990), catastrophes are likely to be less important than small, but sustained reductions in survival and fertility. Pollution in the form of organochlorine contaminants could contribute to such effects (Reijnders 1986). It has also been suggested that environmental contaminants may have an impact on the immune systems of seals and thereby indirectly contribute to increased mortality (Härkönen *et al.* 2006). The simulations clearly demonstrated that an important determinant of persistence in a small subpopulation is the extent of immigration. Thus immigration can counteract local

tendencies toward extinction. Furthermore, the relationship between population dynamics and regulating mechanisms are rarely straightforward; several factors may contribute to changes in a population.

LITERATURE CITED

Allen, S. G., H. R. Huber, C. A. Ribic and D. G. Ainley (1989). "Population dynamics of harbour seals in the Gulf of the Farallones, California." Calif. Fish. Game **75**(4): 224-232.

Andersen, K., S. Des Clers and T. Jensen (1995). Aspects of the sealworm *Pseudoterranova decipiens* life-cycle and seal-fisheries interactions along the Norwegian coast. Pp 557-564 *in* Blix, A., Walløe, L., and Ulltang, Ø. (eds.). Whales, seals, fish and man. Elsevier Science B. V.
.

Andersen, S. (1976). "Marsvinet i danske farvande. Fisk og Hav 75-76." Danmarks Fiskeri- og Havundersøgelser: 53-57.

Bigg, M. A. (1969). "The harbour seal in British Columbia " Bull. Fish. Res. Bd Can. **172**: 1-33.

Bigg, M. A. (1981). Harbour seal *Phoca vitulina* Linnaeus, 1758 and *Phoca largha* Pallas, 1811 Handbook of Marine Mammals. London, Academic Press. **2:** 1-27.

Bjørge, A. (1992). "The reproductive biology of the harbour seal, Phoca vitulina L., in Norwegian waters." Sarsia **77**(1): 47.

Bjørge, A. (1993). The harbour seal, Phoca vitulina L., in Norway and the role of science in management. Bergen, Department of Fisheries and Marine Biology, University of Bergen. **Dr.scient thesis:** 91 s.

Bjørge, A. (1996). "Conservation of Marine Mammal Populations: Single Species Protection or Ecosystem Management?" Wadden Sea Newsletter(2): 7-11.

Bjørge, A., I. Christensen and T. Øritsland (1981). "Current problems and research related to interactions between marine mammals and fisheries in Norwegian coastal waters." ICES C.M.: 1981/N: 18. 10 pp.

Bjørge, A., M. Olsen and J. Prime (1993). Food and Foraging of the Harbour Seal, *Phoca vitulina* L., in Norwegian waters. *in* The harbour seal, Phoca vitulina L., in Norway and the role of science in management. PhD Thesis . , Dept. of Fisheries and Marine Biology, University of Bergen**:** Pp 54-66

Bjørge, A., H. Steen and N. C. Stenseth (1994). "The effect of stochasticity in birth and survival on small populations of the harbour seal *Phoca vitulina* L." Sarsia **79**: 151-155.

Bjørge, A., D. Thompson, P. Hammond, M. Fedak, E. Bryant, H. Aarefjord, R. Roen and M. Olsen (1995). "Habitat use and diving behaviour of harbour seals in a coastal archipelago in Norway." in A.S. Blix, L. Walløe and Ø. Ulltang (eds) Whales, seals, fish and man. Elsevier Science, Amsterdam: Pp 211-223.

Bjørge, A., N. Øien, S. Hartvedt, G. Bothun and T. Bekkby (2002). "Dispersal and bycatch mortality in gray, Halichoerus grypus, and harbor, Phoca vitulina, seals tagged at the Norwegian coast." Marine Mammal Science **18**(4): 963-976.

Bjørge, A., N. Øien, S. Hartvedt and G. Bøthun (2002). "Dispersal and bycatch mortality in gray, *Halichoerus grypus*, and harbor, *Phoca vitulina*, seals tagged at the Norwegian coast." Marine mammal science **18**(4): 963-976.

Bonner, W. N. (1982). Seals and man, a study of interaction University of Washington Press

Bonner, W. N. and S. R. Whitthames (1974). "Dispersal of common seals tagged in the Wash, East Anglia." Journal of Zoology (London) **174**: 528-531.

Bonner, W. N. and S. R. Witthames (1974). "Dispersal of common seals tagged in the Wash, East Anglia." Journal of Zoology (London) **174**: 528-531.

Boulva, J. and I. A. McLaren (1979). "Biology of the harbour seal, *Phoca vitulina*, in eastern Canada." Bull. Fish. Res. Bd Can. **200**: 1-24.

Bowen, W. D., C. K. Chapstick and D. E. Sergeant (1981). "Temporal changes in the reproductive potential of female harp seals (*Pagophilus groenlandicus*) " Can. J. Zool. **38**: 495-503.

Burkey, T. V. (1989). "Extinction in nature reserves: the effect of fragmentation and the importance of migration between reserve fragments." Oikos **55**: 75-81.

Chitty, D. (1960). "Population processes in the vole and their relevance to general theory." Can. J. Zool **38**: 99-113.

Dietz, R., M.-P. Heide-Jørgensen and T. Härkönen (1989). "Mass deaths of harbour seals (*Phoca vitulina*) in Europe." Ambio **18**(5): 258-264.

Drescher, H. E. (1979). "Biologie, Ökologie und Schutz der Seerhunde im Schelswigholsteinischen Wattenmeer." Beitrage zur Wildbiologie. Meldorf. 73p.

Durant, S. S. and J. J. Harwood (1992). "Assessment of monitoring and management strategies for local populations of the Mediterranean monk seal Monachus monachus." Biological conservation **61**(2): 81.

Eberhardt, L. L. (1981). Population Dynamics of the Pribilof Fur Seals *n* C. W. Fowler and T. D. Smith , editors. Dynamics of large mammal populations. John Wiley and Sons, New York.
: pp 197-220.

Folkens, P. A. and R. R. Reeves (2002). Sea mammals of the world London, A. & C. Black.

Fowler, C. W. (1981a). Comparative Population Dynamics in Large Mammals. *Pages* 437-455 *in* C. W. Fowler and T. G. Smith, eds. Dynamics of Large Mammal Populations. John Wiley & Sons, New York.

Fowler, C. W. (1981b). "Density Dependence as Related to Life History Strategy." Ecology **62**(3): pp. 602-610.

Goodman, D. (1987). "Considerations of stochastic demography in the design and management of biological reserves." Nat. Resour. **1**: 205-234.

Goodman, S. J. (1998). "Patterns of extensive genetic differentiation and variation among European harbor seals (Phoca vitulina vitulina) revealed using microsatellite DNA polymorphisms." Molecular Biology and Evolution **15**(2): 104-118.

Hanski, I. (1999). Metapopulation ecology / Ilkka Hanski. New York, Oxford University Press

Hanski, I. and D. Simberloff (1997). The metapopulation approach, its history, conceptual domain and application to conservation, Academic Press, San Diego.

Harding, K. C., T. Harkonen and H. Caswell (2002). "The 2002 European seal plague: epidemiology and population consequences." Ecology Letters **5**(6): 727-732.

Harwood, J. (1981). Managing grey seal populations for optimum stability. *Pages* 159-172 *in* C. W. Fowler and T. G. Smith, eds. Dynamics of Large Mammal Populations. John Wiley & Sons, New York

Harwood, J. and A. Hall (1990). "Mass mortality in marine mammals - its implications for population-dynamics and genetics." Trends Ecol. Evol. **5**: 254-257.

Harwood, J. and J. Prime (1978). "Some factors affecting the size of British greay seal populations." J. Appl. Ecol. **15**: 401-411.

Harwood, J. and P. Rohani (1996). The population biology of marine mammals Pp. 174-190 *in* Frontiers of population ecology. A. W. S. R. B. Floyd, and P. J. De Barro, eds, CSIRO, Melbourne, Victoria, Australia.

Havforskningsinstituttet (2007). Kyst og Havbruk, 2007. Fisken og Havet, Havforskningsinstituttet.

Hedstrøm, Ø. (1994). "Dok.nr.8:05 (1994-1995) Forslag fra stortingsrepresentant Øystein Hedstrøm om å be Regjeringen stoppe kravet om nitrogenrensing av avløpsvann i kommunene." from http://www.stortinget.no/dok8/dok8-199495-005.html.

Heide-Jørgensen, M. P. (1988). Sælernes økologi i Kattegat. Undersøgelser fra 1978 til 1985. Report to the Ministry of Environment from Danibu ApS., Biological Consultants, Denmark.

Heide-Jørgensen, M. P. and R. Dietz (1982). "Sælernes populationsbiologi i Kattegat. Undersøgelser fra 19778-1981." Fredningsstyrelsen, Miljøministeriet. Danske sælundersøgelser i Kattegat **6**: 1-33.

Heide-Jørgensen, M. P. and T. J. Härkönen (1988). "Rebuilding seal stocks in the Kattegat-Skagerrak " Marine Mammal Science **4**(3): 231-246.

Henriksen, G. (2000). "Steinkobbe *Phoca vitulina* langs Skagerrakkysten " Fauna **53**(4): 199-217.

Henriksen, G. and N. Røv (2004). Kystsel : havert og steinkobbe. Trondheim, Tapir.

Hunter, M. L. (2002). Fundamentals of conservation biology / Malcolm L. Hunter, Jr. ; illustrated by Andrea Sulzer.

Härkönen, T. (1987). Feeding ecology and population dynamics of the harbour seal (Phoca vitulina) in Kattegat-Skagerrak. Göteborg, , Department of Zoology.

Härkönen, T. (1987b). "Influence of feeding on haul-out patterns and sizes of subpopulations in harbour seals." Neth. J. Sea Res. **21**(4): 331-339.

Härkönen, T. (1988). "Seasonal and regional variations in the feeding habits of the harbour seal, *Phoca vitulina*, in the Skagerrak and the Kattegat." J. Zool. London **213**: 535-543.

Härkönen, T. (2006). Stockholm, Sweden, Swedish Museum of Natural History.

Härkönen, T. (1987). Site fidelity, migrations and mortality in harbour seals (Phoca vitulina) in the Skagerrak. Paper No VIII in Härkönen, T. 1987 Feeding ecology and population dynamics of the harbour seal (Phoca vitulina) in the Kattegat-Skagerrak, Dr. Thesis at University of Göteborg.

Härkönen, T. (1987a). Site fidelity, migrations and mortality in harbour seals (Phoca vitulina) in the Skagerrak. Paper No VIII in Härkönen, T. 1987 Feeding ecology and population dynamics of the harbour seal (Phoca vitulina) in the Kattegat-Skagerrak, Dr. Thesis at University of Göteborg.

Härkönen, T., R. Dietz, P. Reijnders, J. Teilmann, K. Harding, A. Hall, S. Brasseur, U. Siebert, S. J. Goodman, P. D. Jepson, T. D. Rasmussen and P. Thompson (2006). "A rewiev of the 1988 and 2002 phocine distemper virus epedemics in European harbour seals." Diseases of Aquatic Organisms **68**: 115-130.

Härkönen, T. and K. C. Harding (2001). "Spatial structure of harbour seal populations and the implications thereof." Canadian Journal of Zoology **79**: 2115-2127.

Härkönen, T., K. C. Harding and M. P. Heide-Jørgensen (2002). "Rates of increase in age structured populations: A lesson from the European harbour seals." Can. J. Zool **80**: 1498-1510.

Härkönen, T., K. C. Harding and S. G. Lunneryd (1999). "Age- and sex-specific behaviour in harbour seals Phoca vitulina leads to biased estimates of vital population parameters." Journal of Applied Ecology **36**(5): 825-841.

Härkönen, T. and M. P. Heide-Jørgensen (1990). "Comparative life histories of east Atlantic and other harbour seal populations
" Ophelia **32**(3): 211 -235.

Härkönen, T. and M. P. Heide-Jørgensen (1991). "The harbour seal *Phoca vitulina* as a predator in the Skagerrak." Ophelia **34**(3): 191-207.

Jarvinen, J. and S. L. Varvio (1986). "Proneness to extinction of small populations of seals; Demographic and genetic stochasticity vs. environmental stress." Finn. Game Res. **44**: 6-18.

Jeffries, S., H. Huber, J. Calambokidis and J. Laake (2003). "Trends and status of harbor seals in Washington state: 1978 -1999." Journal of Wildlife Management **67**: 207-218.

Kareiva, P. (1990). "Population dynamics in spatially complex environments: Theory and data." Philosophical Transactions of the Royal Society of London **330**: 175-190.

King, J. E. (1983). Seals of the world Oxford University press.

Krebs, C. J. (1994). Ecology. *The experimental analysis of distribution and abundance*. Harper & Row, New York.

Lett, P. F., R. K. Mohn and D. F. Gray (1981). Density-Dependent Processes and Management Strategy for the Northwestern Atlantic Harp Seal Population. *In* C. W. Fowler and T. D. Smith , editors. Dynamics of large mammal populations. John Wiley and Sons, New York.**:** pp 135-157.

Levins, R. (1969). "Some demographic and genetic consequences of environmental heterogeneity for biological control." Bull. Entomol. Soc. Amer. **15**: 237-240.

Markussen, N. H. (1992). "Apparent decline in the Harbour Seal *Phoca vitulina* population near Hvaler, Norway, following an epizootic." Ecography **15**: 111-113.

Markussen, N. H., A. Bjørge and N. A. Øritsland (1989). "Growth in harbour seals (Phoca vitulina) on the Norwegian coast " J. Zool., London **219**: 433-440.

Matthiopoulos, J., J. Harwood and L. Thomas (2005). "Metapopulation consequences of site fidelity in colonial breeders " Journal of Animal Ecology **74**: 716-727.

McLaren, I. A. (1990). Pinnipeds and Oil: Ecologic Perspectives. Sea Mammals and Oil: Confronting the Risks. J. R. Geraci and D. J. St. Aubin, (eds) Academic Press. Inc.

Olsen, M. and A. Bjørge (1995). "Seasonal and regional variation in diet of harbour seal *Phoca vitulina* in Norwegian waters." in Blix, A., Walløe, L., and Ulltang, Ø. (eds.). Whales, seals, fish and man. Elsevier Science B. V.: Pp. 271-285.

Payne, M. R. (1977). "Growth in a fur seal population." Phil. Trans. Royal Soc. London **279**: 67-79.

Pella, J. J. and P. K. Tomlinson (1969). "A generalized stock production model." Bulletin of the Inter-American Tropical Tuna Commission **13**: 419-496.

Pierce, G. J. and M. B. Santos (2003). "Diet of harbour seals (*Phoca vitulina*) in Mull and Skye (Inner Hebrides, western Scotland)." Journal of the Marine Biological Association of the UK **83**: 647-650.

Pierce, G. J., P. M. Thompson, A. Miller, J. S. W. Diack, D. Miller and R. P. Boyle (1991). "Seasonal variation in the diet of common seals (*Phoca vitulina*) in the Moray Firth area of Scotland " Journal of Zoology **223**: 641-652.

Pitcher, K. W. and D. C. McAllister (1981). "Movements and haul-out behavior of radio-tagged harbour seals." Canadian Field Naturalist **95**(3): 292-297.

Reijnders, P. J. H. (1986). "Reproductive failure in common seals feeding on fish from polluted coastal waters." Nature **324**: 456-457.

Reijnders, P. J. H., M. N. de Visscher and E. e. Reis (1988). "The Mediterranean monk seal." IUCN, Gland.

Reijnders, P. J. H., H. E. Drescher, J. L. van Haaften, E. B. Hansen and S. Tougaard (1982). Population dynamics of the harbour seal in the Wadden Sea. pp 19-32. *in* Reijnders, P. J. H., & Wolf, W. J. (eds) Marine mammals of the Wadden Sea Balkema, Rotterdam.

Reijnders, P. J. H., E. H. Ries, S. Tougaard, N. Nørgaard, G. Heidemann, J. Schwarz, E. Vareschi and I. M. Traut (1997). "Population development of of harbour seals Phoca vitulina in the Wadden Sea after the 1988 virus epizootic." J. Sea Research **38**: 161-168.

Roen, R. and A. Bjørge (1995). "Haul-out behaviour of the Norwegian Harbour seal during summer." in A.S. Blix, L. Walløe and Ø. Ulltang (eds) Whales, seals, fish and man. Elsevier Science: Pp. 61-67.

Sergeant, D. E. (1978). "Research on harp seals in 1978."

Shaffer, M. L. (1981). "Minimum population size for species conservation." BioScience **31**: 131-134.

Summers, C. F. and M. D. Mountford (1975). "Counting common seal." Nature **253**(5494): 670-671.

Svansson, A. (1975). Physical and chemical oceanography of the Skagerrak and the Kattegat. I, Open sea conditions. Lysekil

Thompson, M. P., G. J. Pierce, J. R. G. Hislop, A. Miller and J. S. W. Diack (1991). "Winter foraging by common seals (*Phoca vitulina*) in relation to food availability in Inner Moray Firth, N. E. Scotland " J. Anim. Ecol. **60**: 283-294.

Thompson, P. M. (1988). "Timing of mating in the common seal (*Phoca vitulina*)." Mammal Rev. **18**(2): 105-112.

Thompson, P. M., M. A. Fedak, B. J. McConnel and K. S. Nicholas (1989). "Seasonal and sex-related variation in the activity patterns of common seals (*Phoca vitulina*) " Journal of Applied Ecology **26**: 521-535.

Thompson, P. M., K. M. Kovacs and B. J. McConnel (1994). "Natal dispersal of harbour seals (*Phoca vitulina*) from breeding sites in Orkney, Scotland." J. Zool. London **234**: 668-673.

Thompson, P. M., B. J. McConnel, D. J. Tollit, A. Mackay, C. Hunter and P. A. Racey (1996). "Comparative distribution, movements and diet of harbour and grey seals from the Moray Firth, N. E. Scotland." J. Appl. Ecol. **33**: 1572-1584.

Thompson, P. M. and D. Miller (1990). "Summer foraging activity and movements of radio-tagged common seal (*Phoca vitulina* L.*)* in the Moray Firth, Scotland." J. Appl. Ecol. **27**: 492-501.

Thompson, P. M., D. Miller, R. Cooper and P. S. Hammond (1994). "Changes in the distribution and activity of female harbour seals during the breeding season: implications for their lactation strategy and mating patterns." Journal of Animal Ecology **63**: 24-30.

Thompson, P. M., D. J. Tollit, D. Wood, H. M. Corpe, P. S. Hammond and A. Mackay (1997). "Estimating harbour seal abundance and status in an estuarine habitat in north-east Scotland." Journal of Applied Ecology **34**(1): 43-52.

Tollit, D. J., S. P. R. Greenstreet and P. M. Thompson (1997). "Prey selection by harbour seals, *Phoca vitulina*, in relations to variations in prey abundance." Canadian Journal of Zoology **75**: 1508-1518.

Ugland, K. I., G. Stenmark, M. Anstensrud and L. Ø. Knutsen (1984). "Steinkobbe i Oslofjorden." Fauna **37**: 1-5.

van Haaften, J. L. (1982). "The life history of the harbour seal in the Wadden sea " Reijnders, P.J.H. & Wolff, W.J. (Eds) Marine mammals of the Wadden Sea. Balkema, Rotterdam: 15-19.

Vaughan, R. M. (1978). "A study of common seals in the Wash, East Anglia." Mammal Rev. **8**(1&2): 25-34.

Wiig, Ø. and N. Øien (1988). "Recoveries of common seals, Phoca vitulina L., tagged along the Norwegian coast." Fauna norv. Ser. A, **9**: 51-52.

Wipper, E. (1975). "Jahreszeitige Wanderungen bei Seerhunden." Natur und Museum **105**(11): 346-350 & 375-380.

Øynes, P. (1966). "Sel i Sør-Norge." Fiskets Gang, 1966 **45**: 834-839.

APPENDIX 1

Appendix 1. The numerical values of the three trajectories in the comparisons between the age structured model incorporating density dependence and the logistic model. Three population growth rates are simulated: (a) slow (r = 4.2%), (b) intermediate (r = 6.7%) and (c) fast (r = 10.5%)

Year	Slow Popgrowth Age-structured	r = 0.042 Logistic	Intermediate Popgrowth Age-structured	r = 0.067 Logistic	FastPopgrowth Age-structured	r = 0.105 Logistic
0	20	20	20	20	20	20
1	21	21	22	21	23	22
2	22	22	24	23	25	24
3	23	23	25	24	28	27
4	24	23	26	26	30	30
5	25	24	28	27	33	33
6	25	25	29	29	36	36
7	26	27	31	31	40	40
8	27	28	33	33	44	43
9	28	29	35	35	48	48
10	29	30	37	38	53	53
11	31	31	40	40	58	58
12	32	32	42	43	64	64
13	33	34	45	45	70	70
14	34	35	48	48	77	77
15	36	36	51	51	85	84
16	37	38	54	55	93	92
17	38	39	57	58	102	101
18	40	41	61	62	112	111
19	41	43	64	66	123	121
20	43	44	68	70	135	132
21	45	46	73	74	148	144
22	46	48	77	79	162	157
23	48	50	82	83	177	171
24	50	52	88	89	192	186
25	52	54	93	94	209	202
26	54	56	99	100	227	219
27	56	58	105	106	246	236
28	58	61	112	112	266	255
29	61	63	119	119	287	275
30	63	66	126	126	309	296
31	65	68	134	133	331	318
32	68	71	142	141	355	341
33	71	74	150	149	379	365
34	73	77	159	157	403	389
35	76	79	168	166	428	414
36	79	83	178	176	454	439
37	82	86	188	185	479	465
38	86	89	198	195	505	491
39	89	92	209	206	530	518

Year	Slow Popgrowth Age-structured	r = 0.042 Logistic	Intermediate Popgrowth Age-structured	r = 0.067 Logistic	FastPopgrowth Age-structured	r = 0.105 Logistic
41	96	100	232	228	581	570
42	100	103	244	240	605	596
43	103	107	257	252	629	621
44	107	111	270	265	653	646
45	112	115	283	278	676	670
46	116	120	297	291	697	693
47	120	124	311	305	718	715
48	125	129	326	320	739	737
49	130	133	341	334	758	757
50	134	138	356	349	776	776
51	139	143	371	364	793	795
52	145	148	387	380	810	812
53	150	154	402	396	825	828
54	155	159	418	412	839	843
55	161	165	435	428	853	857
56	167	171	451	444	865	870
57	173	177	467	461	877	881
58	179	183	484	477	887	892
59	185	189	500	494	897	902
60	192	195	516	511	907	912
61	198	202	533	528	915	920
62	205	209	549	544	923	928
63	212	216	565	561	930	935
64	219	223	581	577	936	941
65	227	230	597	594	942	947
66	234	238	613	610	948	952
67	242	245	628	626	953	957
68	250	253	643	642	957	961
69	258	261	658	657	961	965
70	266	269	672	672	965	969
71	274	277	686	687	968	972
72	283	286	700	701	972	975
73	291	294	714	715	974	977
74	300	303	727	729	977	980
75	309	312	739	742	979	982
76	318	321	752	755	981	984
77	327	330	763	767	983	985
78	337	339	775	779	985	987
79	346	349	786	791	986	988
80	356	358	797	802	988	989
81	365	368	807	813	989	991
82	375	378	817	823	990	992
83	385	387	826	833	991	992
84	395	397	835	842	992	993
85	405	407	844	851	993	994
86	415	418	852	859	993	995
87	426	428	860	867	994	995
88	436	438	868	875	995	996

Year	Slow Popgrowth Age-structured	r = 0.042 Logistic	Intermediate Popgrowth Age-structured	r = 0.067 Logistic	FastPopgrowth Age-structured	r = 0.105 Logistic
90	457	459	882	889	996	997
91	467	469	888	896	996	997
92	478	480	895	902	997	997
93	488	490	901	908	997	997
94	499	501	906	914	997	998
95	509	511	912	919	997	998
96	520	522	917	924	998	998
97	530	532	921	929	998	998
98	540	543	926	933	998	999
99	551	553	930	937	998	999
100	561	563	934	941	999	999
101	572	574	938	945	999	999
102	582	584	942	948	999	999
103	592	594	945	952	999	999
104	602	604	948	955	999	999
105	612	614	952	958	999	999
106	622	624	954	960	999	999
107	632	634	957	963	999	999
108	641	644	960	965	999	1000
109	651	654	962	968	999	1000
110	660	663	964	970	999	1000
111	670	672	967	972	1000	1000
112	679	682	969	973	1000	1000
113	688	691	970	975	1000	1000
114	697	700	972	977	1000	1000
115	706	709	974	978	1000	1000
116	714	717	976	980	1000	1000
117	723	726	977	981	1000	1000
118	731	734	978	982	1000	1000
119	739	742	980	984	1000	1000
120	747	750	981	985	1000	1000
121	755	758	982	986	1000	1000
122	763	766	983	987	1000	1000
123	770	774	984	987	1000	1000
124	777	781	985	988	1000	1000
125	785	788	986	989	1000	1000
126	792	795	987	990	1000	1000
127	798	802	988	990	1000	1000
128	805	809	989	991	1000	1000
129	812	815	989	992	1000	1000
130	818	821	990	992	1000	1000
131	824	828	991	993	1000	1000
132	830	834	991	993	1000	1000
133	836	839	992	994	1000	1000
134	841	845	992	994	1000	1000
135	847	851	993	994	1000	1000
136	852	856	993	995	1000	1000
137	858	861	994	995	1000	1000

Year	Slow Popgrowth Age-structured	r = 0.042 Logistic	Intermediate Popgrowth Age-structured	r = 0.067 Logistic	FastPopgrowth Age-structured	r = 0.105 Logistic
139	867	871	994	996	1000	1000
140	872	876	995	996	1000	1000
141	877	880	995	996	1000	1000
142	881	885	995	997	1000	1000
143	886	889	996	997	1000	1000
144	890	893	996	997	1000	1000
145	894	897	996	997	1000	1000
146	898	901	996	997	1000	1000
147	901	905	997	998	1000	1000
148	905	908	997	998	1000	1000
149	909	912	997	998	1000	1000
150	912	915	997	998	1000	1000
151	915	919	997	998	1000	1000
152	918	922	998	998	1000	1000
153	922	925	998	998	1000	1000
154	925	928	998	999	1000	1000
155	927	930	998	999	1000	1000
156	930	933	998	999	1000	1000
157	933	936	998	999	1000	1000
158	935	938	998	999	1000	1000
159	938	941	998	999	1000	1000
160	940	943	999	999	1000	1000
161	943	945	999	999	1000	1000
162	945	947	999	999	1000	1000
163	947	950	999	999	1000	1000
164	949	952	999	999	1000	1000
165	951	954	999	999	1000	1000
166	953	955	999	999	1000	1000
167	955	957	999	999	1000	1000
168	957	959	999	999	1000	1000
169	958	961	999	999	1000	1000
170	960	962	999	1000	1000	1000
171	961	964	999	1000	1000	1000
172	963	965	999	1000	1000	1000
173	964	967	999	1000	1000	1000
174	966	968	999	1000	1000	1000
175	967	969	999	1000	1000	1000
176	968	970	999	1000	1000	1000
177	970	972	1000	1000	1000	1000
178	971	973	1000	1000	1000	1000
179	972	974	1000	1000	1000	1000
180	973	975	1000	1000	1000	1000
181	974	976	1000	1000	1000	1000
182	975	977	1000	1000	1000	1000
183	976	978	1000	1000	1000	1000
184	977	979	1000	1000	1000	1000
185	978	980	1000	1000	1000	1000
186	979	981	1000	1000	1000	1000

Year	Slow Popgrowth Age-structured	r = 0.042 Logistic	Intermediate Popgrowth Age-structured	r = 0.067 Logistic	FastPopgrowth Age-structured	r = 0.105 Logistic
188	981	982	1000	1000	1000	1000
189	981	983	1000	1000	1000	1000
190	982	984	1000	1000	1000	1000
191	983	984	1000	1000	1000	1000
192	984	985	1000	1000	1000	1000
193	984	986	1000	1000	1000	1000
194	985	986	1000	1000	1000	1000
195	986	987	1000	1000	1000	1000
196	986	987	1000	1000	1000	1000
197	987	988	1000	1000	1000	1000
198	987	988	1000	1000	1000	1000
199	988	989	1000	1000	1000	1000
200	988	989	1000	1000	1000	1000